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Determinants of Small Rodent Distribution and Abundance in a Shrub-Steppe Ecosystem: Influences of Seeds, Ants and Shrubs

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DETERMINANTS OF SMALL RODENT DISTRIBUTION AND

ABUNDANCE IN A SHRUB-STEPPE ECOSYSTEM:

INFLUENCES OF SEEDS, ANTS AND SHRUBS

by

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iii

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Finally, to my parents who nurtured and encouraged my explorations in the world of nature, and to Tom Hatton who continues to encourage them, thank you.

Linda Suzanne Broome

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

ixLIST OF FIGURES

FigurePage

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

ABSTRACT

Determinants of Small Rodent Distribution and

Abundance in a Shrub-steppe Ecosystem:

Influences of Seeds, Ants and Shrubs

by

Linda Suzanne Broome, Doctor of Philosophy

Utah State University, 1988

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This study had two major objectives; firstly to test the hypothesis of ongoing competition for seeds between small rodents and harvester ants, Pogonomyrmex occidentalis, in a cold desert ecosystem; secondly to elucidate how seed abundance and shrub cover influence the distribution and abundance of deer mice, Peromyscus maniculatus. The study area was a sagebrush (Artemisia tridentata) dominated shrub-steppe in southwestern Wyoming. Responses of the small mammal community to ant removal and food addition were assessed on replicated study plots between September 1981 and September 1983. Food addition and shrub removal manipulations were continued from September 1983 to August 1984. Rodent populations were sampled by live-trapping. Movements of 40 deermice were followed by radiotracking during the winter, spring and summer of 1983-84.

Ant removal elicited little response from the rodent community, although seed preference trials with native seeds in the field indicated considerable overlap in seed use. I concluded that competition was not a factor affecting small rodents during the period of this study, although the area cleared of ants may not have been sufficiently large to produce a response detectable by trapping.

Seed addition resulted in increased deermouse population size, prolonged breeding, decreased winter (but not summer) home range sizes, and during periods of low density, increased grid fidelity. High fall densities were followed by a classical spring decline with associated female sex ratio skew and severe injuries to both sexes. I concluded that deermice were food limited only to the point where social interactions during the breeding season limited maximum densities.

The absence of shrubs prevented winter use of the 1.25 ha cleared area by deermice. At this time on the non-cleared plots shrubs were used to support nests, as foraging sites and as a means of access to the snow surface. During summer the area cleared of shrubs provided attractive foraging habitat, but most nest sites were still located within shrub cover around the edge.

An important corollary of the radio tracking was the illustration of the large home range sizes of deermice in relation to the size of the 0.7 ha trapping grids. The implications of trapping bias affecting population fluctuations and measurement of other demographic parameters from trapping studies are discussed.

(165 pages)

CHAPTER I

INTRODUCTION

1.1 Objectives

A fundamental theme of population and community ecology is to explain what limits populations, and why individuals are more abundant in some areas than in others. Proximate regulating mechanisms may include interactions with the same or other species (competitors, predators or parasites), and the effects of disease or climate. The intensity, timing, duration and relative importance of these proximate mechanisms are dependent upon environmental factors which prevent unlimited increase. These factors may include extrinsic variables such as the quality and availability of food and cover, and intrinsic variables (or individual quality) such as the physiological, genetic or phenotypic status of individuals (Chitty 1967, Watson and Moss 1970, Krebs 1978). It is now widely accepted that controlled, manipulative field experiments are necessary for elucidation of the relative importance of such influences on animal populations.

This study had two primary objectives. The first objective was to test the prediction that interspecific competition with ants, for seeds, was a regulating mechanism for small rodent populations in a cold desert, shrub-steppe ecosystem. The second objective was to assess the extent to which food and shrub cover were limiting factors for the deermouse (Peromyscus maniculatus) populations in this ecosystem. A third, methodological objective arose as a consequence of

measuring rodent population parameters from trapping data; suspected violations of estimator assumptions led me to evaluate their validity by comparing radiotelemetry and trapping results.

1.2 Interspecific Competition Between Rodents and Ants

Most manipulative studies of competition among granivores have been conducted in hot deserts. Granivorous desert rodents may be influenced by interspecific competition from closely related species (Grant 1972, Schroder and Rosenzweig 1975, Hutto 1978, Stamp and Ohmart 1978, Holbrook 1979, Munger and Brown 1981, Brown and Munger 1985) or from granivorous ants or birds (Brown et al. 1975, Mares and Rosenzweig 1978, Brown et al. 1979a, b, Davidson et al. 1980). By conducting reciprocal removal experiments in the Sonoran Desert, Brown and Davidson (1977), Brown et al. (1979a), Davidson et al. (1980, 1984) attested that population densities of granivorous desert rodents are influenced by interspecific competition from harvester ants (and vice versa in the short term, although ants may be facilitated by the presence of rodents in the long term [Davidson et al. 1984]). In contrast, Brown and Munger (1985), Davidson et al. (1985), found no evidence of competitive effects of ants on rodents in the Chihuahuan Desert. These apparently contradictory results might be due to a combination of inappropriate statistical tests and small sample biases (Galindo 1986), and inadequate grid sizes (Galindo and Krebs 1986). Hot deserts are typified by diverse assemblages of species with a low density of individuals. In the Sonoran Desert study the rodent samples consisted of combined counts of 4 species from 0.1 ha study plots with

a maximum sample size of 13. Five species of small granivorous rodents were combined in the Chihuahuan Desert study, with 2 _Dipodomys_ species counted separately. Fewer than 7 individuals from each of these 3 groups were trapped during each sampling period on 0.25 ha study plots. Even so, the authors suggest that lack of competition between rodents and ants in the Chihuahuan Desert could be due to diffuse compensation and competition between species within each higher taxon (Davidson et al. 1985). In an experimental context it is easier to deal with single species "communities" (_sensu_ MacMahon et al. 1978), or communities having a low species diversity. Fewer potential interactions have to be accounted for and larger sample sizes are generally obtainable for the dominant species. My study area had advantages in this respect for testing interspecific competition between granivorous rodents and ants. Several rodent species were present on the study area but biomass was comprised predominantly of one small mammal species, the deermouse, and only one species of harvester ant (_Pogonomyrmex occidentalis_). Thus, interspecific competition between ants and mice, if it operates in this simple system, should not be masked by interactions between species within each higher taxon.

To infer ongoing competition for a particular resource it is neccessary to demonstrate (1) negative interactions between guild members, (2) overlap in requirements for the resource, and (3) that the resource limits the size of populations (Brown et al. 1979_b_). Thus, the following hypotheses were tested:

1. The addition of seeds does not result in a significant increase in small rodent population size.

4

2. The removal of ants does not result in a compensatory increase in rodent population size.

3. Rodents and ants do not overlap in their use of seed species.

The first two hypotheses were tested by seed addition and ant removal treatments on rodent trapping grids. A reciprocal removal experiment was not attempted due to the scale of the experimental manipulations required to produce statistically testable results, and the difficulty of removing rodents from large, unfenced study plots. Overlaps in seed preferences between rodents and ants were assessed by a field study of granivory, in which a variety of indigenous seed species were offered seperately to nocturnal rodents (predominantly deermice) and ants; diurnal rodents (least chipmunks _Eutamius minimus_) combined with birds were included as part of the competitive milieu.

1.3 Influences of Food and Shrubs on Deermouse Populations

Resource limitation may be manifested through competition with other species, or more commonly through intraspecific interactions. Intraspecific competition can cause population size and structure to fluctuate annually around available resource levels, according to the reproductive status of individuals. These observations have led to various behavioral hypotheses of population regulation (Wynne-Edwards 1962, Chitty 1967, Brown 1969, Watson and Moss 1970, Krebs 1970, 1978, Ostfeld 1985). Studies of microtine populations in temperate grasslands have shown that food and/or cover supplementation generally increases reproductive rates and, at certain times of the annual cycle,

elicits a numerical response but fails to prevent a spring decline in numbers (Taitt and Krebs 1981, 1983, Taitt et al. 1981). It has been suggested that these declines can be attributed to reproductive territoriality and socially induced mortality and dispersal (Krebs 1970, Turner and Iverson 1973, Tamarin 1977, Krebs and Boonstra 1978, Gipps et al. 1985). Manipulations of sex ratio (Redfield et al. 1978), male or female aggressiveness (Krebs et al. 1977, Gipps et al. 1981, Taitt and Krebs 1982), and genotype (LeDuc and Krebs 1975) do not prevent the spring decline. Concurrent manipulations of food, cover and risk of predation lead to the suggestion that both socially induced dispersal and predation may be causal mechanisms for the spring declines in Microtus spp. (Taitt and Krebs 1983). Spring declines sometimes occur in forest populations of Peromyscus maniculatus and P. leucopus (Sadleir 1965, Fairbairn 1977, Sullivan 1979) despite supplemental feeding (Hansen and Batzli 1978, Taitt 1981, Gilbert and Krebs 1981). Fairbairn (1977,1978b) and Taitt (1981) suggest that regulation of breeding density through spacing behavior may also be important for deermice. In all these studies changes in spacing behavior have not been observed directly, but were inferred from trapping and from observations of behavioral encounters in the laboratory.

Responses to supplemental cover have been regarded primarily as a function of reduced predation risk. Reduced predation risk has been confirmed observationally (Taitt et al. 1981) and experimentally (Taitt and Krebs 1983) for Microtus spp. in grasslands, but only indirectly for Peromyscus spp. in shrublands (Thompson 1982b, Kotler 1984).

Parmenter and MacMahon (1983) point out that shrub cover may also ameliorate environmental extremes or provide food resources. Shrubs, in desert ecosystems with sparse grass or forb cover, may also provide nest sites. Additionally, they might be structurally important as snowpack support in areas with continuous winter snow cover. Parmenter and MacMahon (1983) removed shrubs from a study plot within the area in which this study was conducted. They concluded that shrub-related food resources, in addition to shrub architecture (cover), had no effect upon deermouse population parameters. Population monitoring following shrub removal was carried out only between the months of May and September, but they suggested that shrubs may be structurally important in winter.

Few studies have examined the role of food and cover on small mammal populations, over an annual cycle, in a cold desert shrubland. The second objective of this study was to assess how food and shrub cover influence the abundance and distribution of deermice and to determine both population and individual responses to these factors in a strongly seasonal environment. I was interested in the following null hypotheses:

1. Populations of deermice given supplemental food do not differ numerically, reproductively or in demographic structure from populations of non-fed individuals.

2. Home range size and activity of individuals do not differ between fed and non-fed populations, either during winter or during spring and summer.

3. The absence of shrubs alters neither population density nor individual home range size or shape.

4. The presence or degree of a spring decline in population size, following the onset of breeding, is not affected by food supplementation or by shrub removal.

1.4 Trapping Bias

The applicability of the responses (numerical, reproductive or behavioral) obtained from the manipulative approach are dependent upon how well the manipulation simulates a change in an environmental component. Lack of response may indicate that the manipulated variable is not an important limiting factor for the population, or it may reflect failure to appropriately modify a limiting factor. Alternatively, the presence of more than one critical factor may promote a compensatory response to the manipulated variable. For example, a numerical response to supplemental food may be masked by increased predation (Cole and Batzli 1978), or by intensified interspecific competition (Brown and Munger 1985, Davidson et al. 1985).

Even if the manipulation is appropriate there is still the persistent problem of accurately estimating the population parameters of interest. Most small mammal studies rely upon trapping grids to provide estimates or indices of abundance and other population parameters such as dispersal or immigration. Trap locations are also commonly used to define microhabitat use, home range size, and to make inferences regarding spacing behavior between individuals. There has, however, been serious doubt concerning the validity of results obtained

from trapping small mammals. Trapping may not be a satisfactory method for studying home ranges or activity patterns (Sheppe 1967), or microhabitat use (Thompson 1982a). Grid sizes at least 16 times larger than the average home range size may be required for accurate assessment of population density (Bondrup-Nielsen 1983).

Most studies of small mammals implicitly assume that the trapping grid contains the home ranges of most of the population under study. This implies that the "edge effect" is not large and the home range size/grid size ratio is small (Bondrup-Nielsen 1983). Edge effect arises from 2 conditions: attraction of animals from outside the grid, and partial enclosure of the grid by home ranges of animals living near the grid edge. Both conditions add to the size of the "effective area" trapped (Dice 1938, Tanaka 1972, Wilson and Anderson 1985b). It is generally recognized that edge effect does cause bias in density estimates, and various attempts have been made to correct this bias. Most methods involve estimating a boundary strip around the grid from movements between traps on the grid, others are more ad hoc (see Bondrup-Nielsen 1983, Wilson and Anderson 1985a, b for reviews). An assumption of these methods is that movements between traps on a grid are of the same scale as movements outside the grid. This includes older methods such as adding 1/2 the average diameter of an animal's home range to the grid perimeter (Dice 1938) and recent attempts such as adding the mean maximum distance moved (MMDM) between traps to the perimeter (Wilson and Anderson 1985b).

Although acknowledging that bias probably exists, many investigators choose to equate estimates of population size ($\hat{N}$) with an area

approximately the size of the trapping grid, using $\hat{N}$ as an index to density. This would be valid for comparisons between trapping grids or trapping occasions only if the boundary width created by the edge effect was constant.

Other, less-recognized problems with a large edge effect concern homogeneity of treatments applied within the area of a trapping grid, and confounding of experimental replicates. Incorrect conclusions may be reached if it is assumed, incorrectly, that those animals trapped on the grid are experiencing an experimental treatment coincident with the grid area, but are not experiencing conditions outside the experimental area. Large edge effect may also invalidate independance of adjacent replicate grids. Another assumption generally made is that traps are not unduly distorting the normal behavior of individuals. The bias introduced when such assumptions are violated is seldom measurable and often unrecognized. Therefore, the third objective of this study was to evaluate my estimates of population density and the conclusions based on trapping by monitoring the movements and behavior of individual deermice using radiotelemetry.

CHAPTER II

STUDY AREA AND METHODS

2.1 Study Area

The study area is a high-elevation (2103 m) shrub-steppe (West 1983) ecosystem, located on the Kemmerer Mine of the Pittsburg and Midway Coal Division of Chevron USA, Inc., 8 km southwest of Kemmerer, Wyoming (Lat. 41 43°N, Long. 110 37°W). Precipitation is highly variable and falls mostly as snow, with monthly peaks from spring rains in May and June. Mean annual precipitation (1951-1980) at the Kemmerer NOAA station is 230 mm /year, but record precipitation levels occurred during this study (83.3, 33.8, 168.4, 372.6 and 165.3 mm above average for the years 1980-1984 respectively). Monthly precipitation and an index to the depth of the snowpack (derived from measurements taken at the Ecosystem Reconstruction 12-UC study site) for November 1980 - April 1984 are presented in Fig. 1.

The study site is located at the base of a north-south extending cliff on the southeast part of the mine and consists of a series of east-west striking washes and low sandy ridges. Vegetation and soils are described by Parmenter and MacMahon (1983), Kelrick (1988), Kelrick et al. (1986). Estimates of shrub density and the percentage cover of shrubs, grasses and forbs are provided in Table 1. Shrub density and percent cover were estimated from 25, 3 X 7 m plots on each of grids 2, 3, 4, 8 (described in the following section). Shrub cover estimates were made by assigning to each shrub a geometric shape and measuring
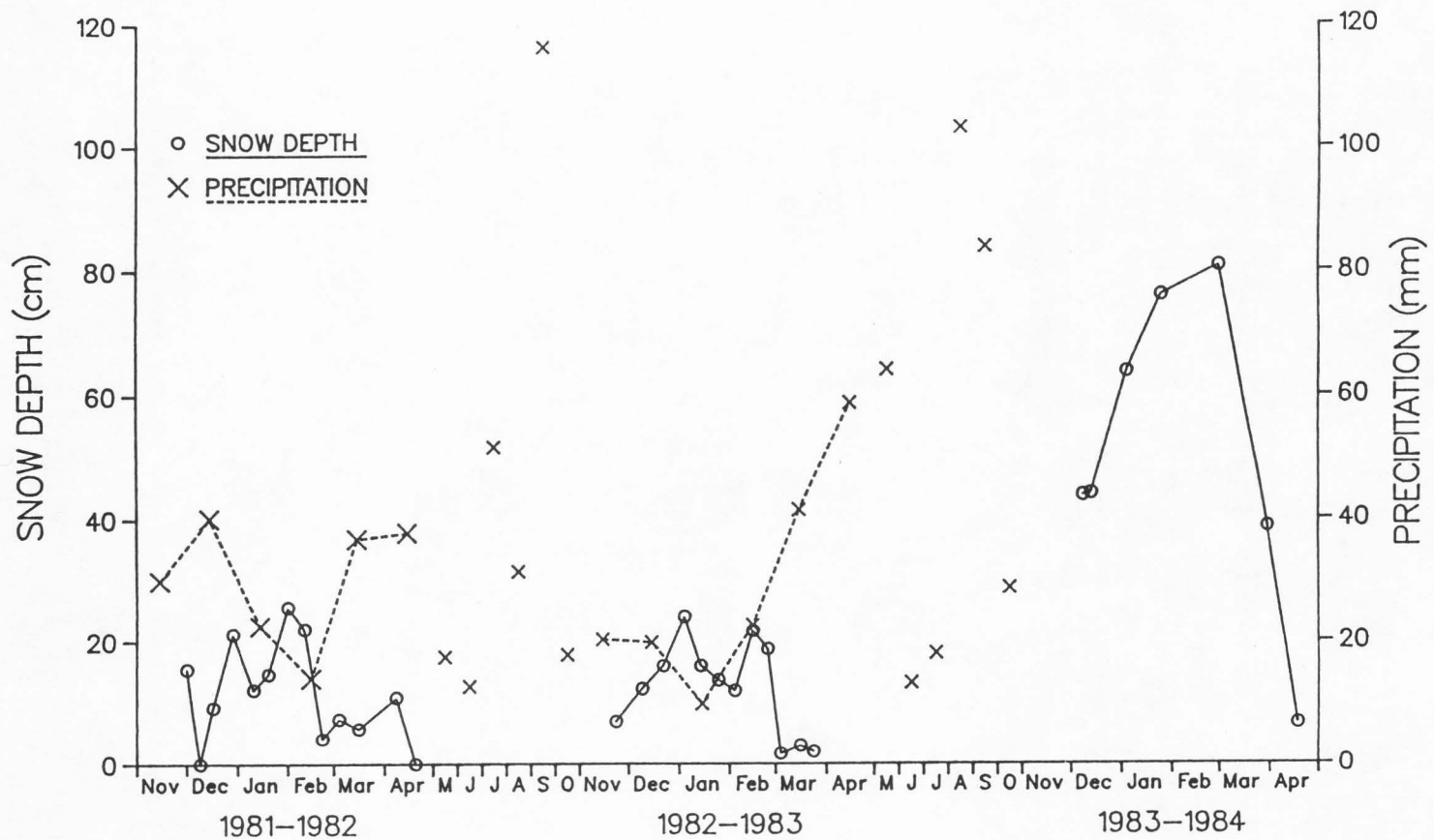
Fig. 1. Index of snow depth on the study area, and monthly precipitation (Kemmerer NOAA station), November 1981 – April 1984.

Table 1. Estimates of shrub density and percent cover of shrubs, grasses and forbs. Shrub measurements from grids 2, 3, 4, 8. Grass and forb cover estimates for grids 7, 8 and the shrub-removal grid.

Shrubs	Density (#/ha) $\overline{X} \pm$ SD	% Cover $\overline{X} \pm$ SD
Sagebrush	7,000 ± 1,795	10.41 ± 2.62
Rabbitbrush	11,443 ± 2,986	2.59 ± 0.83
Other	3,205 ± 967	1.60 ± 0.89
Total	21,590 ± 3,605	14.60 ± 4.14

Grasses & forbs	% cover $\overline{X} \pm$ 2 S.E.	LSD†
Grid 7	22.08 ± 3.21	a
Grid 8	27.36 ± 4.72	ab
Shrub-removal		
Aug. 1980*	19.02 ± 4.12	a
Aug. 1981*	31.50 ± 5.71	b
Sept. 1983	55.74 ± 6.12	c

† Analysis of variance for grass and forb cover:

Source	df	MS	F
Grids	4	10607	35.51 ** (p 0.01)
Error	245	299	
Total	249		

Pooled 95% C.I. (for LSD tests) = 4.79

* Sampled by Parmenter (1982)

the relevant dimensions. The most abundant shrubs are big sagebrush (*Artemisia tridentata*) and rabbitbrushes (*Chrysothamnus viscidiflorus* and *Chrysothamnus nauseosus*). "Other" (Table 1) includes winterfat (*Ceratoides lanata*), gray horsebrush (*Tetradymia canescens*), buckwheat (*Eriogonum microthecum*) and occasional individuals of antelope bitterbrush (*Purshia tridentata*), Gardner saltbush (*Atriplex gardneri*) and cryptantha (*Cryptantha flavoculata*). The percent cover of grasses and forbs was estimated from projected Ektachrome slides. Slides were taken on grids 7, 8 and the shrub-removal grid in September 1983 of 1 m2 plots placed systematically at every second trapping grid stake (50 plots per grid). Similar slides, taken at random locations by Parmenter (1982), were used to provide a comparison of % cover of grasses and forbs on the shrub-removal grid in August 1980 (at the conclusion of removing shrubs) and one year later, in August 1981. Slides from all grids were mixed randomly before ocular cover estimates (Hatton et al. 1986) were made by a single independent observer.

2.2 Interspecific Competition Between Rodents and Ants

Seed addition and ant removal.--Hypotheses concerning interspecific competition between rodents and ants were addressed between September 1981 and September 1983. The first two hypotheses were tested by a two-way factorial experiment, using presence or absence of supplemental food and of ants as the two main variables. This design was replicated and one additional control plot was established, resulting in a total of nine study plots. The plots, 0.71 ha in size (delimited by 13 X 13 station rodent trapping grids with 7m between

traps), were located on the slopes of sandy ridges extending over 2.4 km. Grids 1 to 5 extended from the crest of a ridge down the south facing slope to the washes; grids 6 and 8 were placed similarly on north facing slopes, but also spanned part of the wash; grid 7 covered both sides of a very low ridge with a slope to the west; grid 9 was on top of a level plateau. Treatments, assigned randomly to these grids, are summarized in Table 2; also presented are number of ant mounds in September 1981 and the distances between grids.

Supplemental food, millet (Panicum miliaceum), was provided from September 1981 to November 1982. Sixteen feeding stations, 14 m apart, were established on each of the four fed grids. Feeders were 1 gallon plastic bottles with four holes cut near the bottom and stoppered with halved film canisters to prevent seed spillage. Feeders were placed on inverted plastic plates and raised on wire legs to prevent ants from removing seed. Feeders were continually replenished and the amount of seed removed was recorded.

Ant mounds on and within 20 m of the perimeter of ant removal grids (1.54 ha) were poisoned with Diazinon (Geigy Corporation). Mounds were encircled with metal flashing to prevent rodents from taking the poison. Ants had ceased above ground activity when food was added in September 1981, so were poisoned as they became active in June 1982.

Seed preference.--Tests of seed-use overlap involved seed selection experiments in the field. Indigenous seed species were offered seperately to ants, nocturnal rodents, and diurnal rodents (chipmunks) and birds. Seeds were obtained from Native Plants of Utah, Inc., Salt

Table 2.   The assignments of treatments to the nine study grids, with the
numbers of ant mounds on each grid, and the inter-grid distances.

Grid #	Ant mounds (#)	Treatment	Distance to next grid (m)
1	33	Control	
			180
2	42	Food	
			200
3	27	Food-Ants	
			370
4	42	Food-Ants	
			275
5	26	Control	
			130
6	31	- Ants	
			90
7	28	Control	
			272
8	51	Food	
			135
9	46	- Ants	

16

Lake City, UT, and were chosen to represent a range of the most common grasses, forbs and shrubs which grow on the study area. Two seed mixtures of six species each were supplied in three seperate feeding trials. Mix 1 consisted of 2 g each of four grasses and two forbs: Indian ricegrass (Oryzopsis hymenoides), cheatgrass (Bromus tectorum), green needlegrass (Stipa viridula), Canby bluegrass (Poa canbyi), wild buckwheat (Eriogonum heracleoides) and cicer milkvetch (Astragalus cicer). Mix 2 represented the common shrubs in the area and contained big sagebrush (Artemisia tridentata), rubber rabbitbrush (Chrysothamnus nauseosus) and winterfat (Ceratoides lanata). Poa, Astagalus and Eriogonum (1.5 g/sp.) were also included in this mixture to provide a basis for comparison of preference rankings between the two seed mixtures. Stipa viridula and Astragalus cicer do not grow on the study area but they represent genera present. Dates and duration of each trial are summarized in Table 3.

Seed preference trials for ants were conducted on grid 7 in a 60 X 60 m area which contained 15 ant mounds. The first trial of seed mixture 1 was offered at 25 of 50 randomly chosen locations adjacent to 64 possible trapping grid intersections. Twenty-five of these locations were used in the analysis of seed preference. Those chosen represented locations which had been used by ants but were not so heavily depleted that few seeds remained. These same 25 locations were used for the second trial of mixture 1, but due to shortage of seed only 20 were used with seed mixture 2. The seed mixtures were offered in cardboard bowls, placed in flower pots, and covered with 6.4 mm mesh, hardware cloth to prevent rodent access. These ant dishes were buried

Table 3.   Dates and duration of seed preference trials for seed mixture 1 (grasses and forbs) and seed mixture 2 (shrubs).

Faunal assemblage	Mixture 1 - Rep. 1		Mixture 1 - Rep. 2		Mixture 2	
	Date	Duration	Date	Duration	Date	Duration
Ants	20-21 July 1982	1 day	21-24 Sept. 1982	3 days	13 July 1983	1 day
Nocturnal rodents	19-23 Aug. 1982	4 nights	21-22 Sept. 1982	2 nights	12-14 July 1983	3 nights
Diurnal rodents/ birds	19-23 Aug. 1982	4 days	21-22 Sept. 1982	2 days	12-14 July 1983	3 days

so that the lip of the bowl was flush with the ground surface. The area around the dish was smoothed and cleared of debris. Seeds were placed in the dishes on the morning of each trial before ants became active and were left until the majority of dishes had been used. On all trials for both ants and rodents the remaining seeds were collected after approximately 50% of the seeds had disappeared but before each dish was emptied. Seeds discarded adjacent to the dishes were collected with forceps and placed with the remaining seed. Ant activity peaked in July so it took only one day to achieve 50% seed removal for the first replicate of mixture 1, and for mixture 2. Ants foraged less in September. Therefore, three days were required for replicate 2 of seed mixture 1 (Table 3). Dishes were covered at night during this period. Ant movements and their activities at mounds and dishes were watched closely during the first feeding trial. Ants taking seeds from each dish were followed to their mounds. Mounds were checked the following day to see if any seeds had been discarded at the mound site.

Rodent feeding trials were conducted on grid 1 for seed mixture 1 but were moved to grid 7 for seed mixture 2. The same number of dishes was used with each trial as described for ants, but dishes were located randomly at one of the 169 grid intersections of the full trapping grid. Each location consisted of paired dishes, one for nocturnal rodents the other for diurnal rodents and birds. These dishes were smooth plastic, disposable bowls with down-curving lips that were inaccessible to ants, as confirmed by observation close to ant mounds. Dishes were placed on the ground surface, anchored by heavy nails and surrounded by three small rocks to provide access for rodents. A dish

cover was switched between each pair at dawn and dusk to restrict access to the appropriate taxon. Spilled seeds were replaced in the dishes when the covers were switched.

Seeds were removed to the laboratory, sorted into the component species and weighed. The amount of each species removed was calculated for each dish by subtracting the weight remaining from that initially provided. Assumptions of this technique are detailed by Kelrick et al. (1986).

Rodent population sampling.--Trapping was conducted over four consecutive nights with 169 Sherman live traps on each 13 X 13 station grid. Traps were insulated with cotton batting and baited with peanut butter and rolled oats. Animals were individually marked by toe clipping. On all captures, mice were sexed, checked for reproductive condition (females: pregnant, lactating or with perforate vaginas; males: presence of scrotal testes) and weighed prior to release. Because insufficient traps and personnel were available to trap all nine grids concurrently, the two study design replicates were trapped over consecutive four day periods. Grids 4, 5, 7, 8 and 9 were trapped during the first four days, grids 1, 2, 3, and 6 during days five to eight. The beginning dates of these 8-day trapping periods were 9th September 1981, 21st March 1982, 17th June 1982, 19th August 1982, 14th October 1982, 8th April 1983 (trapping was attempted on the 16th March but was terminated by a heavy snowfall), and 9th September 1983.

2.3 Analysis

Trapping.--Trapping data were analyzed for the purpose of popula-
tion size estimates using program CAPTURE (White et al. 1978). This
program tests a series of capture probability models against each data
set to determine goodness-of-fit. The models allow for heterogeneity
in capture probabilities between individuals (Model h), change in
capture probability after first capture (behavior-Model b), or both
(Model bh). Model t tests for time effects although estimators are not
available for time effects combined with behavior or heterogeneity.
The models all assume that rodent populations are demographically and
geographically closed, that individuals do not lose their marks and
that all marks are correctly noted at each trapping occasion (Otis et
al. 1978). The model best fitting each data set was used to estimate
population size ($\hat{N}$) and a 95 % confidence interval. In five cases the
data were such that no model was appropriate, thus $\hat{N}$ was not estimated
and these were treated as missing cells in the analysis of variance.

Initially, density ($\hat{D}$) was estimated using program HRDEN (K. R.
Wilson, personal communication). Half the mean maximum distance moved
(MMDM), also estimated by CAPTURE, was added to the grid boundary to
estimate the effective area trapped $\hat{A}(W)$ (Wilson and Anderson 1985b).
MMDM is the average of the maximum distance between recaptures for all
animals caught at least twice during a trapping period (Otis et al.
1978). However, as will be demonstrated under objective three (Chapter
1.4), MMDM was a biased estimator of animal movements. Consequently,
comparison between treatments was made using $\hat{N}$. Numbers caught were
consistently large enough to enable use of CAPTURE (greater than ap-

proximately 20 individuals) only for deermice. Therefore, an index to population size, (total number of individuals caught during the four day trapping period), was used for other species.

Treatment effects were analyzed using program RUMMAGE (Bryce 1980), a program which accomodates unbalanced analysis of variance with missing cells. A factorial split plots-in-time design was used. Two analyses were run. In the first, the $\hat{N}$'s were weighted by their standard errors, taking into account the precision of each estimate. In the second, the unweighted $\hat{N}$ was used as the response variable, because the variance estimates from CAPTURE tend to increase with the size of $\hat{N}$ (D. R. Anderson, personal communication).

Seed preference.--The weights of each seed species removed were converted to preference indices ($\hat{P}_i$) relative to the other five species within each dish. $\hat{P}_i$ was calculated using a simple preference metric (Kelrick et al. 1986).

$$\hat{P}_i = \frac{U_i/A_i}{\sum\limits_{i=1}^{k} U_i/A_i}$$

where i = seed species 1, . . . ,k

U_i = grams of seed species i utilized,

and A_i = grams of seed species i available.

Since A_i was a constant, this reduces to

$$\hat{P}_i = \frac{U_i}{\sum\limits_{i=1}^{k} U_i}$$

A split plots analysis of variance, with dishes as plots, was used to test for significant differences in seed preference between granivore categories and seed species, for each seed mixture.

Seed preference by ants as a function of distance.--Distances from each ant mound to the dishes being used by these ants were calculated from a map of the study site. Of the 50 dishes placed during trial 1, 11 were not found by ants. The remaining 39 were used for the following analyses: a) regression of the total amount of seed removed per dish (utilization) against distance from the mound; b) categorization of these distances into 4 intervals (3.0, 3.1 - 6.0, 6.1 - 9.0, 9.1 m) and examination of preferences for each seed species by distance interval.

Results and discussion of the rodent/ant competition study are presented in Chapter III.

2.4 The Influence of Food and Shrubs on Rodent Populations

Experimental manipulations and population responses.--In Chapter IV, I examine the numerical, reproductive and demographic responses of the deermouse populations to food supplementation between September 1981 and September 1983 and concurrently report the results of the second part of the study, which began in September 1983 and continued until August 1984. In the latter period I continued to more inten-

sively monitor population responses on two fed and two non-fed grids (grids 2, 8 and 1, 7 respectively) throughout the winter and spring. Additionally, I examined the role of shrub cover on deermouse distribution and abundance by reinstituting trapping of a 1.25 ha study plot adjacent to grid 4, henceforth designated grid G. This site had been cleared of shrubs in 1980 (Parmenter and MacMahon 1983).

Trapping methods are as described in section 2.2. However, when examining the reproductive condition in males, note was taken of the presence of perianal pouches (Stewart and Brooks 1977) as well as scrotal testes. Four-day trapping periods began on 27th October 1983, 23rd March 1984 and 12th June 1984. Trapping was conducted for two days only on grids 1, 2, 7, and 8 and 3 days on grid G between the 2nd and 12th February 1984, when snow cover averaged 30 cm on grids 7 and 8, 20 cm on gid G, but had virtually melted on grids 1 and 2. A second two day trapping session on all five grids was conducted between 9th-18th May. Both of these trapping periods were initiated to capture mice for radiotracking on grids 7, 8 and G. In August, trapping was carried out for three days on grids 7 and 8.

Supplemental feeding began following trapping in September 1983 and was continued, ad libitum, through June 1984. Twenty-five feeders, 14 m apart, were positioned on grids 2 and 8.

Snowtracking.--Snowtracking was used as an alternate index, unbiased by the presence of traps, of mouse population activity on the three radiotracking treatment grids (7, 8, G). Each concentric square, formed from contiguous grid rows from the perimeter to the center of a grid (6 squares on a 13 x 13 grid), was walked and note taken of the

number of mouse tracks crossing the line between each grid stake. Conditions conducive to such counts occurred on 13 November 1983, 21 December 1983, and 12 February 1984.

Individual activity patterns and use of space.--Radiotelemetry was used to monitor responses of known individuals to the food and cover manipulations. Radiotelemetry enabled the definition of home range sizes independent of trapping locations, and was useful when trapping was not feasible or might be biased during periods of heavy snow cover. Telemetry also enabled documentation of activity patterns, nest site locations and incidents of predation. One non-fed, one fed and the shrub-removal grid (grids 7, 8 and G respectively) were selected for the telemetry study. Grid 7 was extended by 28 m on the western edge and reduced by 14 m along the northern edge (17 X 11 trapping stations) so that it resembled the topography on grids 8 and G.

Radiotelemetry equipment included pretuned 150-152 MHz SM-1 transmitters of different frequencies (AVM Instrument Co., Livermore CA.), multi-channel radio receivers (AVM LA-12 and Telonics TR-2) and hand-held yagi antennas. Transmitters were equipped with hearing-aid batteries (Eveready E312E), encapsulated in Elvax paraffin (Mini-Mitter Co., Sunriver, Oregon) and were surgically implanted into the animal's abdominal cavity (I.P.) through an incision in the ventrolateral abdominal wall (Mineau and Madison 1977, Dr. J. O. Wolff, personal communication). Mice were anaesthetized with a 1:5 mixture of Xylazine/Ketamine HCL (100 mg/ml concentration) using 0.01 cc / 10 g body weight. Each transmitter unit weighed approximately 2 g (10 % of the animal's body weight) and had an average battery life of 30 d.

Transmitter-implanted mice were released on the evening following cap-
ture at their original capture sites and given several days to re-
adjust.

For the duration of a tracking period each mouse was located daily
in its nest. Methods of recording night locations varied slightly
according to weather conditions and the mouse's proximity to the trap-
ping grid. In winter, when snow covered shrubs and other identifiable
features, the observer fixed a signal direction and took a compass
bearing from a tall stake (placed at every second grid stake), then
moved 90 degrees and took a second bearing. Locations were later
identified on a map of the grid by triangulation. If a mouse stayed
for some time at the same location, the exact point was confirmed from
several directions and an identified pin flag left in place after the
mouse moved. During summer, on-grid locations were recorded directly
as distances and directions from grid stakes. All off-grid locations
were identified by pinflags, following triangulation of the position
using a flashlight to identify landmarks. Pinflag locations were
mapped in relation to the grid during daylight. Each observer tracked
4 to 6 mice per night, locating each mouse sequentially. Thus, for a
single mouse, intervals between successive locations were usually at
least 20 min. If a particular behavioral observation was of interest,
a mouse was followed continually and locations were taken every 5 min.
or less. In winter, forays away from the nest site on non-fed grids
were so rare that once a mouse was found away from its nest it was
followed continually until it returned to its nest. Mice did not
appear to be disturbed by an observer moving slowly and quietly, even

at distances as close as 10 m. Flashlight-use was kept to a minimum, but occasionally a mouse was watched by flashlight. Usually these mice continued normal activity unhindered.

At least 25 independent locations (defined as 20 min or more apart) away from its nest site were sought for each mouse, though this was not always possible. During winter, mice were transmitted for up to 30 days and tracked for up to 15 nights. In summer only 4-6 nights of tracking were needed to obtain the desired number of locations (60). Tracking usually commenced at dusk in winter (1700-1800 hrs) and con-tinued until 2400 - 0200 hrs. One all-night session and several early morning tracking sessions were conducted. In summer, timing of tracking periods was variable, with the aim of sampling throughout the night. Often tracking was conducted from dusk until dawn.

2.5 Analysis

Population responses.--Population size ($\hat{N}$) was estimated as des-cribed in section 2.2. Treatment effects (food vs. no food) for the four fed and five non-fed grids trapped between September 1981 and September 1983 were identified by analysis of variance (section 2.2). Population size estimates with 95 % confidence intervals for the five grids studied between September 1983 and August 1984 are presented seperately and compared graphically. Numbers caught during the two days of trapping in February and May were compared to numbers caught during the first two days of trapping during September, October, March and June. An approximation for $\hat{N}$ was obtained by extrapolation.

Demographic parameters (reproduction, sex ratio, injuries, grid

fidelity, new captures) were also analyzed seperately for the two parts of the study (2 treatments and 3 treatments respectively). These parameters were tabulated as binomial response variables (breeding/non-breeding, male/female, injured/non-injured etc.) and analyzed by fitting logit models to the observed cell frequencies (Nie 1983). Independent variables were treatment or grid (depending on whether grids were combined within treatments), date and sex. Frequency tables were simplified, where possible, by collapsing over variables. Chi-square tests were used to test for differences between grids within the September 1981 - September 1983 fed and non-fed treatments (4 and 5 grids respectively) prior to fitting the logit models to the combined data for each treatment. Use of the combined data was necessary because sample sizes from individual grids were often too small to use the logit models. This was not the case for the five grids trapped between September 1983 and June 1984. Comparisons between the levels of each variable were made using contrasts which were orthogonal and summed to zero (I found this was necessary in contradiction to the documentation of the program, Nie 1983:548).

Snowtracking data were analyzed using the same program with a log linear model. MMDM's on each grid were compared by analysis of variance using program RUMMAGE (Bryce 1980).

Activity patterns and use of space.--Home range size and use patterns were estimated by program HOMERANGE (Samuel et al. 1985b). Harmonic means (Dixon and Chapman 1980) were used to specify utilization contours and to identify core areas within the home range (Samuel et al. 1985a). Home ranges are presented graphically using the contour

representing 75% of an animal's utilization distribution. Default grid cell sizes were used for all mice except for winter mice on grid 8, where a 5 m cell size was used because default values were smaller than the error polygon. Additionally, grid cell sizes of 10 m were used where default values were greater than 20 m (mouse numbers 3503, 4036, 4401, 3556).

CHAPTER III

INTERSPECIFIC COMPETITION BETWEEN RODENTS AND ANTS:

RESULTS AND DISCUSSION

3.1 Results

The rodent community.--In this study deermice were the most abun-
dant nocturnal rodents (Fig. 2) and least chipmunks (Eutamius minimus)
were the most numerous diurnal rodents (Fig. 3). Few Great Basin
pocket mice (Perognathus parvus) or northern grasshopper mice
(Onychomys leucogaster) occurred on any grid (Figs. 4 and 5). The
maximum number caught during any trapping period was 9 and 7, respec-
tively. Several non-granivorous, microtine species were also trapped;
sage voles (Lagurus curtatus), montane voles (Microtus montanus) and
long-tailed voles (M. longicaudus). Microtus were trapped infrequently
throughout the study. Sage voles were relatively abundant in 1983/84
(Fig. 6).

Rodent responses to food and ants.--Analysis of variance for food
and ant effects on deermouse population sizes (weighted analysis,
Table 4) indicate that deermice are food limited (rejection of
hypothesis 1, P= .00 for FD). Fed population sizes were greater than
non-fed populations during all trapping periods when supplemental food
was present (P < .01, Table 4), Fig. 2. Population sizes did not
differ when food was not present (P > .2). The overall effect of
removing ants was not significant (P = .599 for AD, Table 4). There is
some evidence that deermice responded to ant removal during the final
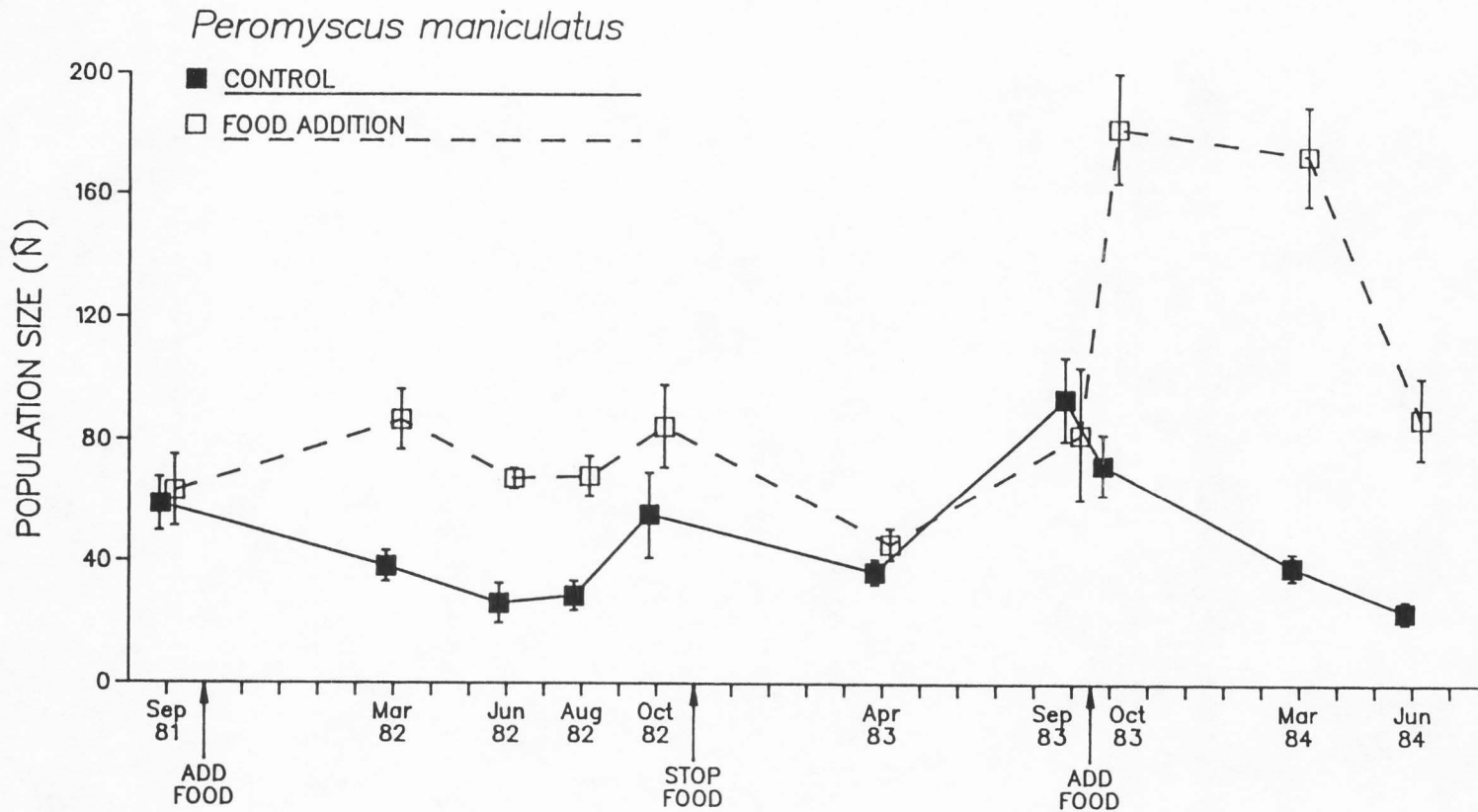
Fig. 2.   Mean population size estimates (with 95 percent confidence intervals) of deermice (Peromyscus maniculatus)on fed and non-fed grids.   September 1981 – September 1983 non-fed grids n = 5, fed grids n = 4; October 1983 – June 1984   n = 2 for both treatments; August 1984 n = 1 for both treatments.
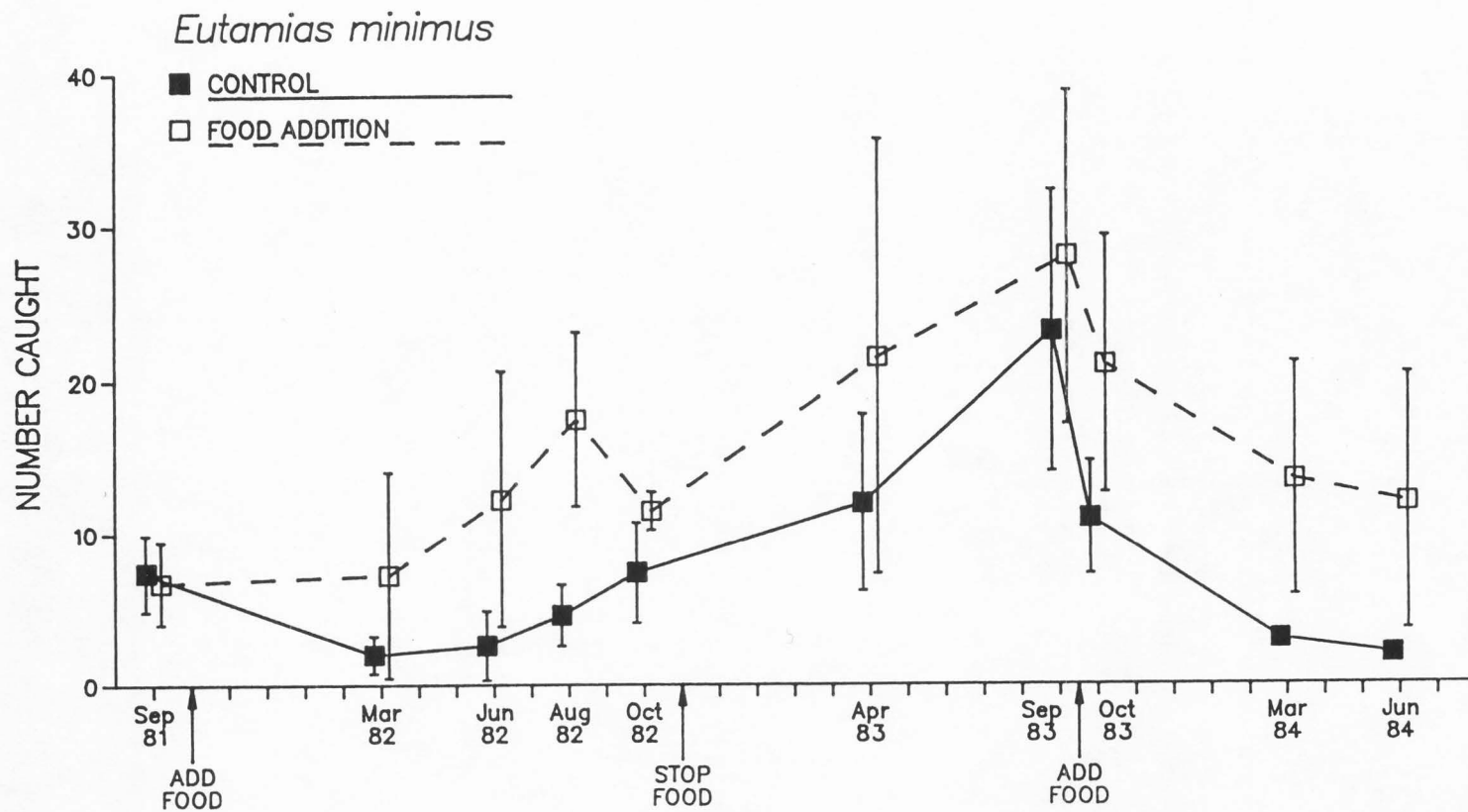
Fig. 3. Mean numbers caught (with 95 percent confidence intervals) of least chipmunks (Eutamias minimus) on fed and non-fed grids. September 1981 – September 1983 non-fed grids n = 5, fed grids n = 4; October 1983 – June 1984 n = 2 for both treatments.
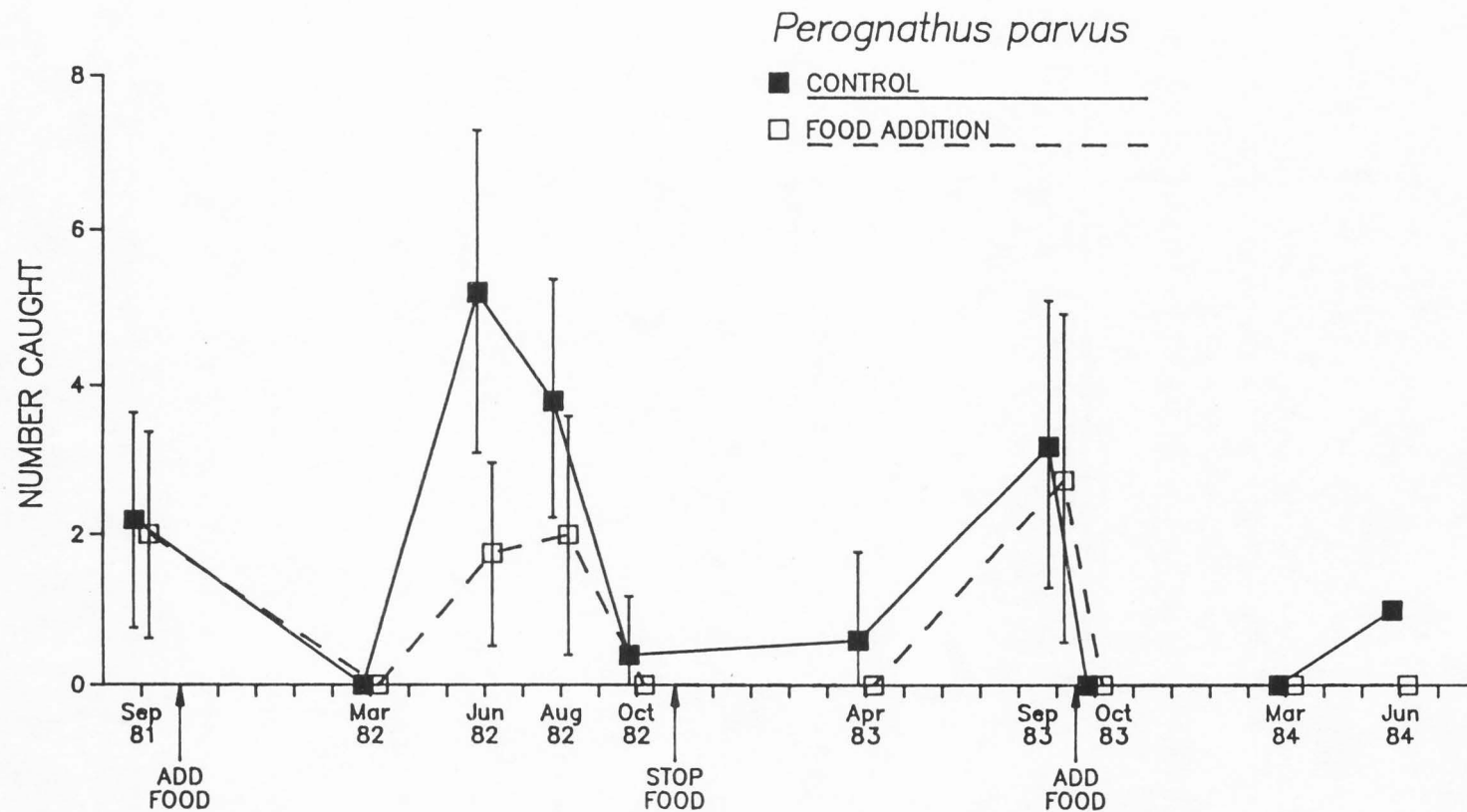
Fig. 4. Mean numbers caught (with 95 percent confidence intervals) of Great Basin pocket mice (Perognathus parvus) on fed and non-fed grids. September 1981 - September 1983 non-fed grids n = 5, fed grids n = 4; October 1983 - June 1984 n = 2 for both treatments.
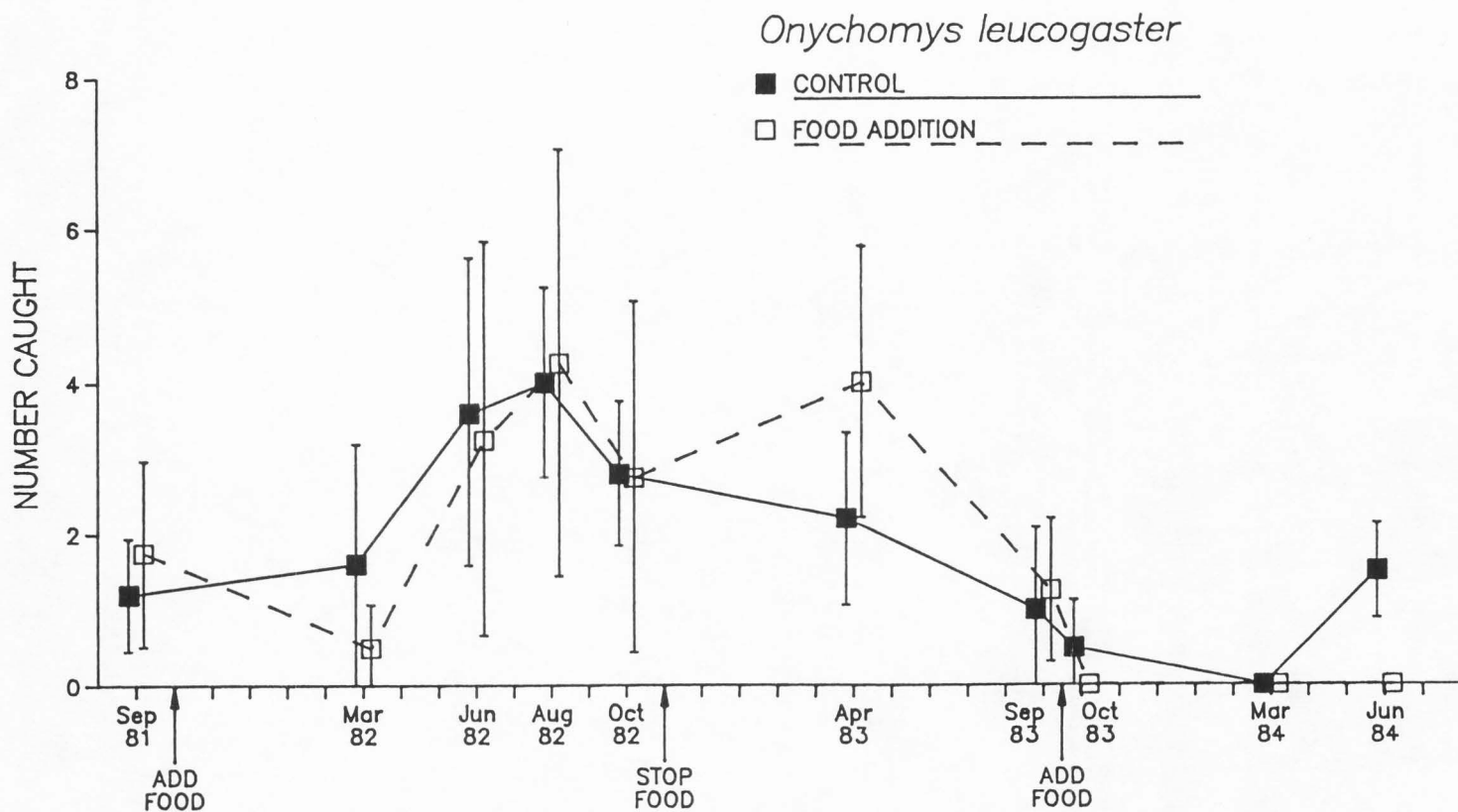
Fig. 5. Mean numbers caught (with 95 percent confidence intervals) of northern grasshopper mice (Onychomys leucogaster) on fed and non-fed grids. September 1981 – September 1983 non-fed grids n = 5, fed grids n = 4; October 1983 – June 1984 n = 2 for both treatments.
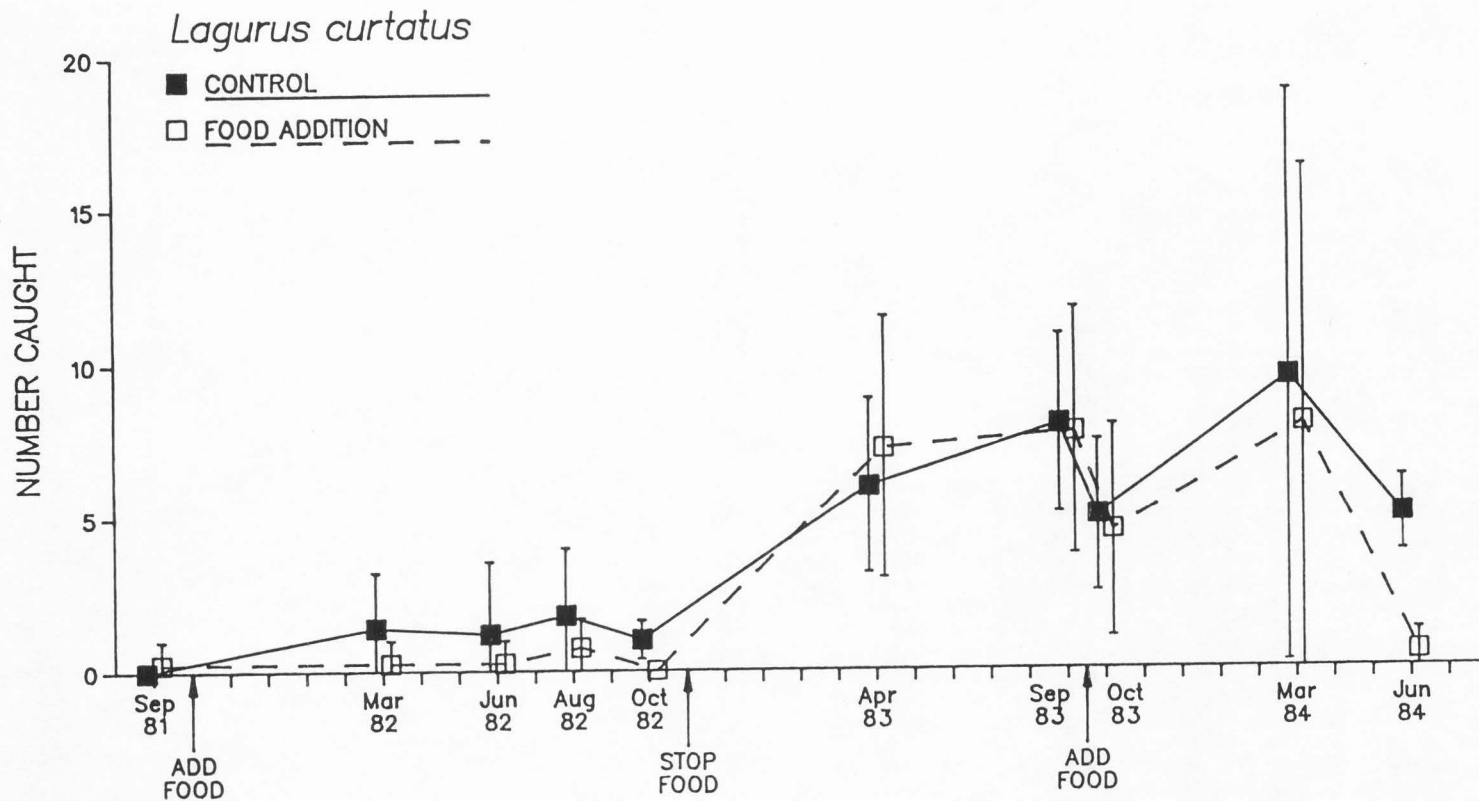
Fig. 6. Mean numbers caught (with 95 percent confidence intervals) of sage voles (<u>Lagurus</u> <u>curtatus</u>) on fed and non-fed grids. September 1981 – September 1983 non-fed grids n = 5, fed grids n = 4; October 1983 – June 1984 n = 2 for both treatments.

Table 4. Analysis of variance (weighted) for ant and food effects on deer-mouse population numbers: September 1981 - September 1983. Significance levels: * = 0.05, ** = 0.01, (*) = 0.10.

Source of variation	df	F-ratio	probability	significance level
Ant (A)	1	0.616	0.468	NS
Food (F)	1	6.257	0.054	(*)
AF	1	0.335	0.588	NS
Grid (G) = error (a)	5	7.825	0.000	**
Date (D)	6	15.149	0.000	**
AD	6	0.773	0.599	NS
FD	6	6.709	0.000	**
AFD	6	0.905	0.507	NS
error (b)	25			

Comparison	Food x Date and Ant x Date comparisons		
	t-value	probability	significance level
Ant x Date			
AD_1	0.756	0.457	NS
AD_2	0.651	0.521	NS
AD_3	0.278	0.776	NS
AD_4	0.378	0.709	NS
AD_5	0.778	0.444	NS
AD_6	0.569	0.574	NS
AD_7	2.046	0.051	(*)
Food x Date			
FD_1	0.977	0.338	NS
FD_2	5.004	0.000	**
FD_3	3.313	0.003	**
FD_4	3.595	0.000	**
FD_5	4.129	0.001	**
FD_6	0.711	0.483	NS
FD_7	1.314	0.201	NS

sampling period, in September 1983 (P = .051 for AD_7). Contrary to prediction, this response was not one of compensatory increase. Deermice were less abundant on the ant removal grids than they were on grids with ants present. This result is tenuous because the significance level was less in the unweighted analysis (P = .113 for AD_7). Significance levels produced for all other factors on the unweighted analysis were very similar to those from the weighted analysis shown on Table 4.

Since sample sizes of other rodent species were small, no significant responses to ant removal were evident. A small positive response to supplemental food was shown by least chipmunks (Fig. 3). In contrast, pocket mouse numbers tended to decrease when food was added (Fig. 4), particularly in June 1982 when they were most numerous on the study area. Grasshopper mice (Fig. 5) and sage voles (Fig. 6) showed no response to supplemental feeding.

Seed preference.--The 3 granivore categories (ants, nocturnal rodents, diurnal rodents and birds) were not mutually exclusive in their preference for seeds (non-significant main effect for granivores, Tables 5 and 6). Some overlap in preference for seeds in both seed mixtures is indicated by significant granivore by seed interactions. These preferences are illustrated for mixture 1 averaged over months (Fig. 7) and for mixture 2 (Fig. 8).

Interactions between months, seeds and granivores (mixture 1, Table 5) were due to differences in strengths of preference for different seed species, although the rank order of preference was similar for each month (Table 7). Nocturnal rodents preferred Oryzopsis,

Table 5. Analysis of variance of seed preference indices for seed
mixture 1 (grasses and forbs). Significance levels: ** = 0.01.

Source of variation	df	F-ratio	probability	significance level
Month (M)	1	0.05	0.823	NS
Dish (D)	24	0.62	0.910	NS
MD	24	0.77	0.764	NS
Granivore (G)	2	0.95	0.390	NS
MG	2	0.23	0.795	NS
Error (a)	96			
Seed species (S)	5	193.45	0.000	**
GS	10	103.10	0.000	**
MS	5	5.13	0.000	**
MGS	10	16.68	0.000	**
error (b)	720			
Total	899			

Table 6. Analysis of variance of seed preference indices for seed mixture 2
       (shrubs). Significance levels: ** = 0.01.

Source of variation	df	F-ratio	probability	significance level
Dish (D)	19	0.72	0.760	NS
Granivore (G)	1	1.90	0.184	NS
Error (a)	19			
Seed species (S)	5	27.40	0.000	**
GS	2	42.35	0.000	**
Error (b)	190			
Total	239			
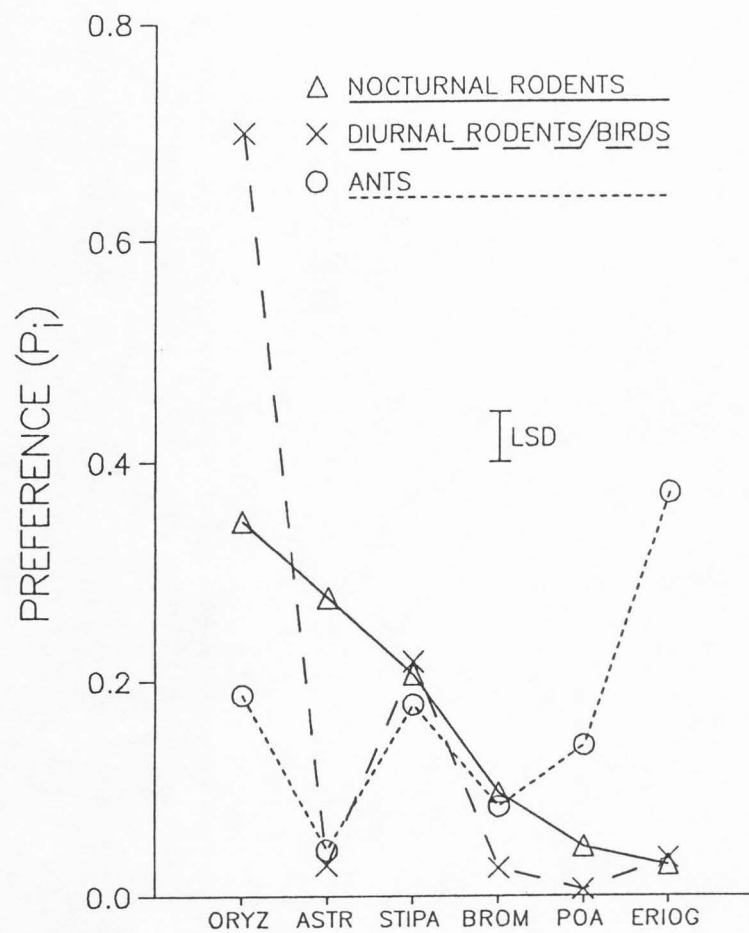
Fig. 7. Preference (mean P_i per dish) by granivores for seeds in mixture 1.
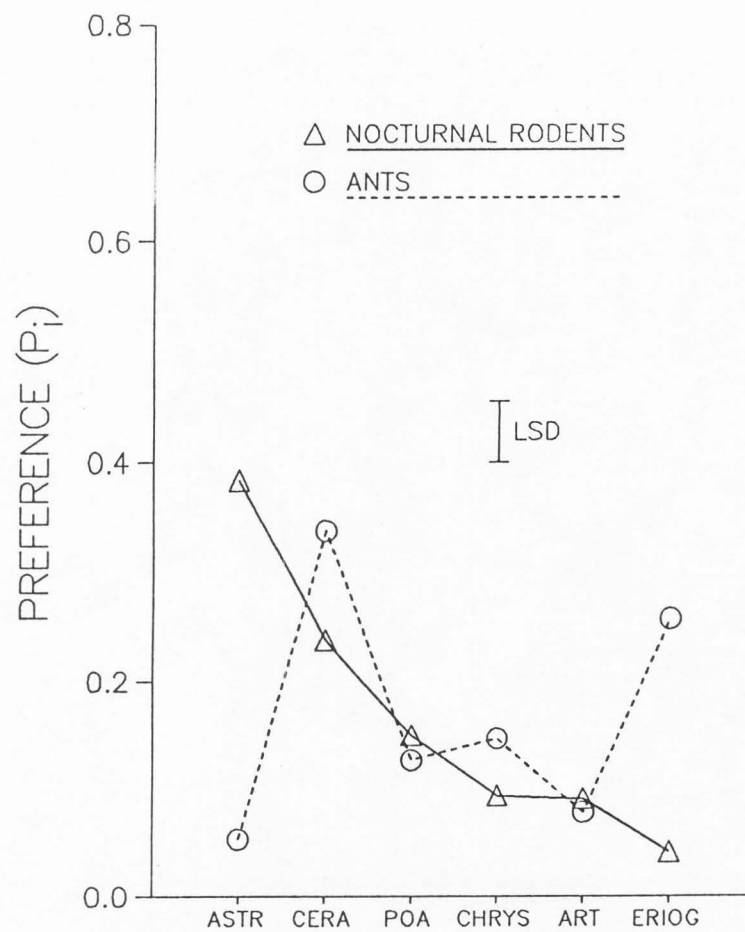
Fig. 8. Preference (mean P_i per dish) by granivores for seeds in mixture 2.

Table 7. Seed preference ranks and results of LSD tests for differences in preference of seeds in mixture 1 (grasses and forbs). A common letter indicates no significant difference in preference ($p < 0.05$).

Seed	Nocturnal Rodent				Diurnal Rodent				Ant			
	Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2	
	rank	LSD	rank	LSD	rank	LSD	rank	LSD	rank	LSD	rank	LSD
Oryzopsis	1	a	1	a	1	a	1	a	2	a	2	b
Astragalus	2	b	2	a	3	c	4	c	6	c	6	d
Stipa	3	c	3	a	2	b	2	b	3	ab	3	b
Bromus	4	d	4	b	5	c	3	c	5	c	5	cd
Poa	5	dc	5	c	6	c	6	c	4	b	4	bc
Eriogonum	6	e	6	c	4	c	5	c	1	a	1	a

followed by Astragalus and Stipa in August; in September they did not discriminate among these seeds (Table 7). In contrast, ants were more selective in September, e.g., $\hat{P}_i$ for Eriogonum in August was 0.25 increasing to 0.50. Astragalus seed was removed by ants in August but not in September (Table 7). Diurnal rodents and birds showed no difference in preference between months. They highly preferred Oryzopsis, moderately preferred Stipa and avoided the other seed species (Fig. 7).

Preferences for seeds in mixture 2 (Fig. 8) were determined only for nocturnal rodents and ants. The preference rankings of the three shrub species, relative to those seeds used in mixture 1, indicate that ants highly prefer Ceratoides, moderately prefer Chrysothamnus and Poa and avoid Artemisia and Astragalus. Rodents moderately prefer Ceratoides but avoid Chrysothamnus and Artemisia.

The effect of distance on seed preference by ants.--The total utilization of seeds (g removed) from each of the 39 dishes found by ants in trial 1, is plotted as a function of distance from the mound in Fig. 9a. The mean utilization of each seed species (g per dish) and the preference for each species (dishes combined) are presented, by distance interval, in Fig. 9b.

3.2 Discussion

Seed preference.--The preference rankings (in descending order) of Oryzopsis, Stipa, Bromus and Artemisia are similar between granivore categories, and correspond to the results obtained by Kelrick et al. (1986). Other studies suggest that Oryzopsis hymenoides seeds are a favored food item for heteromyid rodents (Johnson and Jorgensen 1981,
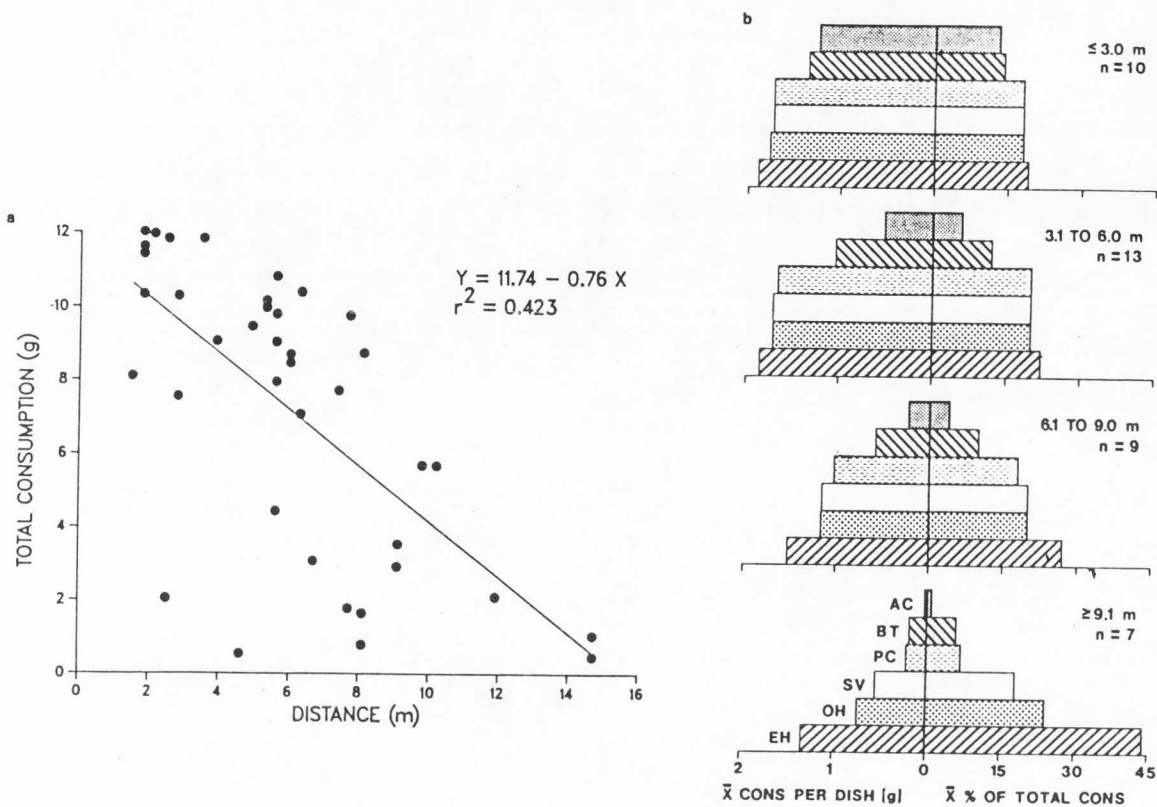
Fig. 9. Seed utilization and selectivity by ants as a function of distance from the mound. Rodent-proof seed dishes containing 6 species of native seeds were offered to Pogonomyrmex occidentalis ants during a 24-h period. Distance = length of a straight line between a particular seed dish and mound center of the colony harvesting seeds from that dish. (a) A regression of total consumption (= all seed types) on distance. Regression coefficient b is significant (P < 0.005, df = 37). (b) Histograms portraying, by species, mean consumption per dish (left of 0) and mean contribution to total consumption (right) for 4 distance classes. Distance class intervals were chosen to distribute numbers of observations roughly equally among the intervals. As distance increases, total consumption decreases and selectivity becomes more pronounced. EH Eriogonum heracleoides, OH Oryzopsis hymenoides, SV Stipa viridula, PC Poa canbyi, BT Bromus tectorum, AC Astragalus cicer; CONS consumption.

McAdoo et al. 1983). Feeding experiments indicate that <u>Bromus</u> <u>tectorum</u> seeds are not highly preferred (Everett et al. 1978), but they are consumed by deermice (Johnson 1961, Kritzman 1974), and may be an important food item at times for the Great Basin pocket mouse (La Tourette et al. 1971, Kritzman 1974). I frequently found <u>B.</u> <u>tectorum</u> seeds in granaries of ant mounds (unpublished data) but biomass and numbers of other species, including <u>Poa</u> spp. were greater. <u>Artemisia</u> <u>tridentata</u> seeds were next to last in preference by both ants and nocturnal rodents. On a preliminary analysis, I did not find <u>Artemisia</u> seeds in ant mounds, nor have they been found in the stomachs of deermice trapped in sagebrush habitats (Williams 1959, Johnson 1961).

Kelrick et al. (1986) found that preference was generally corre-lated with seed caloric and % soluble carbohydrate content, but nutri-tional attributes alone did not explain the rankings of <u>Oryzopsis</u>, <u>Stipa</u> and <u>Bromus</u>. It was suggested that interactions with seed anatomy and size may explain the observed differences. In this study, I included 5 seed species for which the nutritional attributes are un-known (<u>Poa</u>, <u>Eriogonum</u>, <u>Astragalus</u>, <u>Chrysothamnus</u> and <u>Ceratoides</u>). The preference rankings of 2 seed species by nocturnal rodents and ants were opposed. <u>Eriogonum</u> was the least preferred seed for nocturnal rodents but second only to <u>Ceratoides</u> for ants. <u>Astragalus</u> was least preferred by ants, but was second only to <u>Oryzopsis</u> for nocturnal rodents. Davidson et al. (1985) found that seeds of <u>E.</u> <u>abertium</u> were used almost exclusively by ants in the Chihuahuan Desert. It is not known if rodents actually consumed <u>Astragalus</u>, but Everett et al. (1978) found that deermice removed (and presumably consumed) <u>A.</u> <u>cicer</u>

in the lab and preferred it above B. tectorum. Ants did remove some Astragalus but most of this was discarded on ant mounds. A combination of secondary chemical compounds and physical attributes might account for this strong difference in seed preference. For example, ants may have difficulty handling the smooth, dense seeds of Astragalus, while rodents may be deterred by chemical compounds in Eriogonum.

Other authors have suggested that seed size may partially account for differences in seed preference between rodents and ants. Rodents tend to select larger seeds than ants (Inouye et al. 1980, Mittlebach and Gross 1984, Davidson et al. 1984, 1985). The preference for the small Poa seeds by ants but not by rodents might be attributable to seed size. Clearly, more than size is involved with the other seed species. Ceratoides was the largest seed offered in my experiments but was more highly preferred by ants than by rodents. Oryzopsis, Astragalus and Eriogonum were of a similar size but differed greatly in preference ranking between taxa. Chrysothamnus seeds were large but were preferred even less than Poa by rodents. Chemical compounds might account for these differences.

The relative contributions of chipmunks and birds to the diurnal granivore component was not determined. These granivores removed as much millet during the supplemental food study in June and July 1982 as nocturnal rodents did (unpublished data). Observations of low numbers of birds in the study area leads me to believe that much of this was due to chipmunks (which are known to cache seed). This belief is supported by the highly selective removal of Oryzopsis, with some Stipa, but negligible quantities of Poa (or any other species) from the

seed preference trials. Best (1972) found a high proportion of <u>Poa</u> <u>secunda</u> seeds in the diets of Brewer's and Vesper sparrows, together with seeds of <u>Stipa</u> <u>viridula</u> and <u>S.</u> <u>comata</u>. Why chipmunks (or birds) should not take <u>Astragalus</u>, which was a preferred seed for nocturnal rodents is unknown.

Temporal differences in the degree of seed selectivity by nocturnal rodents may be related to the overall importance of seeds in their diet. Seeds formed a higher proportion of the diet of deermice in August than in July 1981 (Parmenter and MacMahon 1983). Records kept during this study indicated that the amount of millet removed from feeders during the food supplementation experiment increased in fall. Both deermice (<u>personal observation</u>) and chipmunks (Nowak and Paradiso 1983) cache seed. The lower degree of selectivity in September compared to August might be a reflection of greater caching activity and decreasing availability of natural seeds (L. S. Broome, <u>personal observation</u>; Kelrick 1988) and other sources of food, including invertebrates (Parmenter and MacMahon 1984).

Seed selectivity by ants increased as a function of distance from the mound (Fig. 9). This observation is consistent with an optimal foraging strategy for central place foragers (Orians and Pearson 1977). Their greater selectivity in September, compared to August, coincides with substantially reduced worker activity and cooler surface temperatures. Greater selectivity indicates that a high payload was required for efficient foraging in September.

<u>Interspecific competition between rodents and ants</u>.--Density compensation by rodents was not demonstrated upon removal of ants, despite

overlap in seed preference; although deermice, and perhaps chipmunks, were shown to be food limited. Possible contributing factors are:

1. A low impact by ants on the seed resource. This is unlikely considering the high density of ant mounds in the area, the rapid rate of removal of seeds by ants during summer feeding trials, and the high predation by harvester ants on seeds reported in other studies (Brown et al. 1979b and citations therein, Reichman 1979, Inouye et al. 1980).

2. The food limitation indicated by supplemental millet experiments was not indicative of the situation actually experienced on ant removal plots. Millet seed is greatly preferred over any native seed found on the study area (Parmenter et al. 1984, Kelrick and MacMahon 1985, Kelrick et al. 1986). Although preferences for seeds such as Oryzopsis, Stipa and Bromus did coincide for ants and rodents, the quantities of these or other species of seeds released by the removal of ants may have been insignificant. Oryzopsis was not abundant on the study area, and seeds removed from ant mounds contained a greater proportion of small-seeded species, such as Poa spp., Chenopodium spp. and seeds of the family Brassicaceae, than of Oryzopsis or Bromus. Limitation by means other than by food (Chapter 5), in the presence of seeds less preferred than millet, may have prevented a numerical response to ant removal.

3. High background food levels were promoted by the unusually wet conditions throughout the study. Wet seasons induce high seed productivity (Noy-Meir 1973, Pulliam and Brand 1975, Inouye et al. 1980) and probably elevate numbers of arthropods. Both seeds and arthropods are included in the diets of deermice and chipmunks (Johnson

1961, Halford 1981, Parmenter and MacMahon 1983). Interspecific competition, if it occurs in a shrub-steppe environment (Rotenberry 1980), might be important only in years of drought (Pulliam and Brand 1975, Weins 1977).

4. It is very likely that the area cleared of ant mounds (1.54 ha) was too small to enable detection of a rodent response by trapping. Home range sizes of deermice averaged 0.31 ha on control grids in summer, so few mice would be resident within the grid area (Chapter 4.2). Traps and food drew animals in from a great distance outside the trapping grid and the area cleared of ant mounds. This effect would prevent detection of small responses to ant removal.

These results are consistent with those obtained in the Chihuahuan Desert (Brown and Munger 1985, Davidson et al. 1985), but contrary to results from the Sonoran Desert (Brown and Davidson 1977, Brown et al. 1979a, Davidson et al. 1980, 1984). Brown and Munger (1985) and Davidson et al. (1985) attributed their differences to greater intensity of competition and compensatory responses within each of the more diverse assemblages of each taxon in the Chihuahuan Desert, and to less dietary overlap between rodents and ants. Compensatory responses were not evident among the most abundant rodents in my study. Differences in dietary overlap, and in the faunal assemblage and seed milieu may lead to competition in the Sonoran Desert, but not in this study area. However, the evidence presented for density compensation by rodents upon removal of ants in the Sonoran Desert is weak, and does not stand up to reanalysis (Galindo 1986). Sample sizes and grid sizes were probably inadequate for robust statistical analysis (Galindo and Krebs

1986, Chapter 4.3, this study). As Galindo points out, the average differences between control and ant-removal treatments on the Sonoran Desert study plots amount to only one individual of the four combined species.

Some evidence of a compensatory response to food supplementation was found for the least abundant granivorous rodent in this study. Admittedly, the evidence is weak, but Fig. 4 indicates that Great Basin pocket mice decreased in abundance when food was added. Competition from deermice, which increased in abundance, might have induced this decrease. Supplemental food had no effect on northern grasshopper mice, which are highly insectivorous (Johnson 1961, Horner et al. 1964), or on the graminivorous sage voles (Johnson 1961, Maser et al. 1974, Maser and Strickler 1978).

Davidson et al. (1984) suggested that in the long-term, granivorous rodents may indirectly facilitate ants by reducing competition among their preferred food plants. This study suggests that the presence of harvester ants may facilitate deermice. Fewer deermice were trapped in the absence of ants during the final trapping period of the ant removal treatment in September 1983. Explanations of this relationship are speculative, but may include effects of ants on the plant community as well as the physical presence of ant discs. Radiotelemetered mice (Chapter IV) were frequently observed close to ant mounds. They may simply have been foraging in the dense vegetation which grew on the perimeter of some discs (presumably induced by moisture runoff from mounds and perhaps discarded seeds). They may also have been searching mounds for seeds discarded by ants; ants discarded non-

preferred seeds, particularly <u>Astragalus</u> and <u>Bromus</u>, on top of their mounds during the seed selection experiment. Predation by mice of seed stores within ant mounds (Clark and Comanor 1973) was not observed for native seeds, but mounds which had millet seeds stored in them were torn apart.

In summary, this study did not demonstrate ongoing competition for seeds between rodents and ants. Rodents were food-limited, but compensatory increases in rodent numbers were not obtained upon removal of ants despite overlap in seed preference. In view of the large home range sizes of radiotracked deermice (Chapter 4.2) I suspect that ants were removed from an area too small to enable detection of any compensatory responses. Previous tests of ant-rodent competition may suffer from similar insufficiencies. Since food preferences did overlap, interspecific competition may occur during years of drought.

CHAPTER IV

INFLUENCES OF FOOD AND SHRUBS ON DEERMICE:

RESULTS AND DISCUSSION

4.1 Population Responses to Food Addition and Shrub Removal

Population size.--Population size estimates for the 2 phases of
trapping are presented in Fig. 10. For the September 1981-September
1983 trapping period common means ($\hat{N}$) and variances (var. ($\hat{N}$) = $\sum^n_{i=1}$
se^2/n^2, D. R. Anderson, personal communication) were estimated for the
four grids on which food was supplied and the five non-fed grids.
Population size was significantly greater on fed grids at all times
when food was present, and not significantly different between fed and
non-fed grids when food was absent (Chapter 3). Similarly, for the two
fed and two non-fed grids trapped between September 1983 and August
1984, population size was greater on fed grids at all times when food
was present. The response to feeding was extremely rapid; numbers had
almost doubled by October 1983, five weeks following food addition in
September.

Numbers declined over winter on non-fed grids during each of the
three years, and continued to decline between March and June, after
breeding had commenced. A spring decline occurred on fed grids despite
the abundance of food; and was also present on the shrub-removal grid
in 1984. Overwinter population sizes in 1983/84 differed between the
two fed grids and between the two non-fed grids. This may relate to the
onset of snowmelt. Grids 1 and 2 were snow free by 2 February but 30
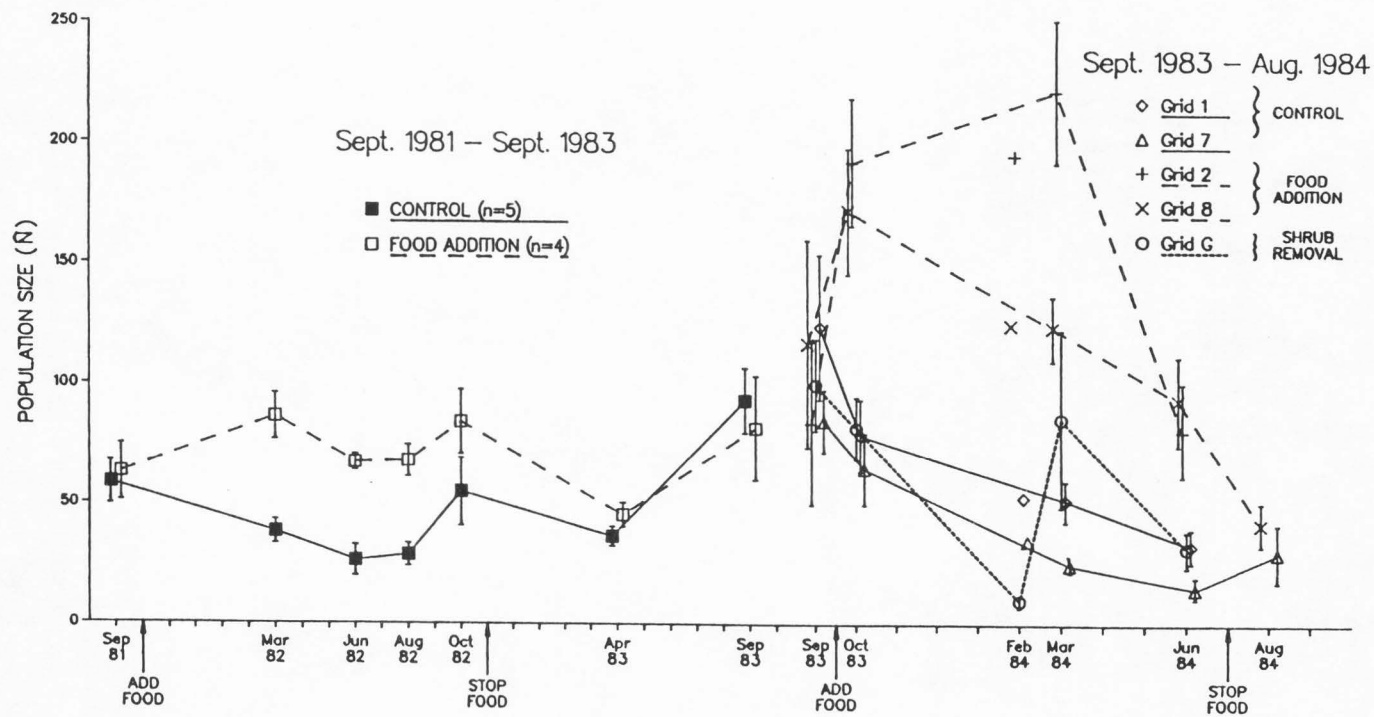
Fig. 10. Population size estimates (with 95% confidence intervals) on combined fed and non-fed grids for September 1981 – September 1983; and for separate food-addition and control grids and the shrub-removal grid from September 1983 – August 1984.

52

cm still covered grids 7 and 8, small patches remained until 23 March.

Numbers declined on grid 8 throughout the winter and spring paralleling

the control grids. Using the extrapolations of $\hat{N}$ in February and May

it appears that these declines occurred principally in two pulses;

during the severest part of the winter (October to February) and in the

latter part of spring (May - June). On grid 2 there was no evidence of

an overwinter decline; however, a precipitous spring decline occurred

between March and June. The slight increase seen in March may have

been due to an influx of mice following the early February snowmelt.

An undetected winter decline could have occurred between October and

January.

Population sizes on the shrub-removal grid are also illustrated in

Fig. 10. Compared to the non-fed grids (pooled), population sizes on

the shrub-removal grid declined to extinction when snow was present,

increased in March (Z=2.56, P=.01), but otherwise were not signifi-

cantly different (P>.05). The grid was repopulated in March at fall

levels, but a significant spring decline occurred. Mice were not able

to use the grid when it was snow-covered. During the February 10

trapping period 10 cm of snow still covered most of the grid but had

begun to melt in the northeast corner. The few mice caught were all in

this corner, or in traps on the perimeter of the grid.

Demographic analysis.--The following demographic analyses are made

from the numbers of individuals caught, subdivided according to grid,

sex and age. These data are presented for combined fed and combined

non-fed grids and the shrub-removal grid in Table A1. Mice 13 g or

less were designated juveniles, 14 - 16 g subadults, and 17 g or

heavier, adults. Growth curves indicate that Peromyscus weigh 13 g at approximately 4 wk of age (Layne 1968, Hansen and Batzli 1978, Millar et al. 1979) and are weaned between 3 and 4 wk of age (Stebbins 1977, Millar et al. 1979). Most mice weighing 13 g or less had juvenile pelage (grey). The subadult and adult weight classes are combined for the analysis of sex ratio, grid fidelity and grid turnover rates. These age classes were difficult to distinguish, and bias may arise if a weight criterion is used under two different feeding regimes. Breeding condition is considered only for sexually mature individuals. Stebbins (1977) indicated that sexual maturity of female P. maniculatus, given unlimited food in a semi-natural situation, was reached at a mean weight of approximately 17 g and 6 wk of age. Males may attain sexual maturity soon after entering the trappable population at weights less than 17 g (Millar et al. 1979). Therefore, all individuals designated as adults (17 g) are deemed potentially reproductive and are considered in the analysis of breeding status.

Sex ratio.--Sex ratios of adults and subadults combined were influenced by supplemental food and varied seasonally on both fed and non-fed grids (Fig. 11; logit model tests are presented in Table A2). Significantly higher proportions of females occurred in fed compared to control populations during spring. These ratios did not differ from August to October. Binomial tests (Zar 1974) indicated that there was a significant sex-ratio skew from parity towards females on fed grids in spring (when most animals were adults). In fall (October 1982), the skew for adults and subadults was towards males. The female skew in spring was attributable to adults only; sex ratios of subadults on fed
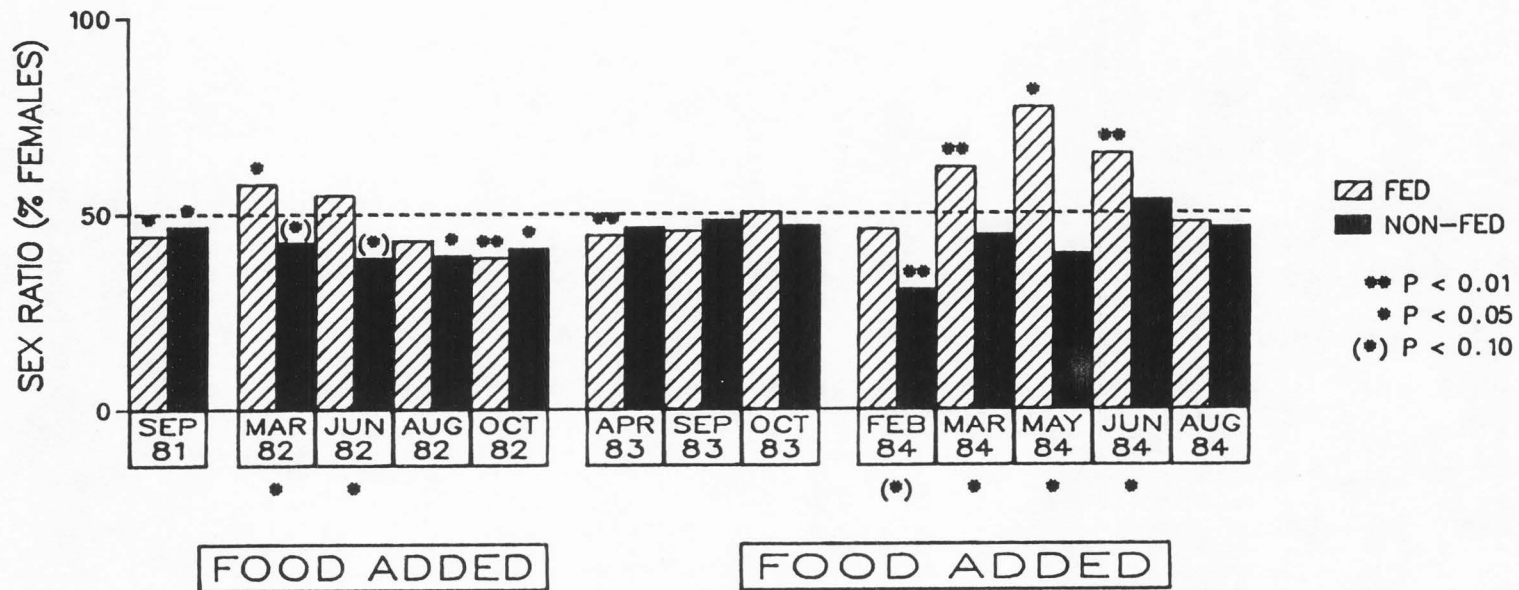
Fig. 11. Sex ratios of adults and subadults (percent females) on fed and non–fed grids. Significance levels from logit model tests between treatments (lower), and binomial tests for differences from a ratio of 50 percent (upper).

grids were male-biased in June and August 1982 (binomial test: Z=2.935, P <.01), and were even or tended toward male bias in June and August 1984 (Table A1). By contrast, on non-fed grids and on fed grids when food was absent the skew was always towards males (Fig. 11).

It is shown in Table 8 that sex ratios of juveniles tended to differ between fed and non-fed grids during spring but not during fall (monthly data were pooled to increase sample size). The male skew on fed grids during spring was significant (binomial test: Z=2.77, P<.01).

On the shrub-removal grid sex ratios of adults and subadults did not differ significantly from parity during any of the trapping periods between September 1983 and June 1984. The ratio was very close to 50% during all months. (n=6, X2 = 51.23, sd = 4.35). Thus, in spring 1984 the shrub-removal grid differed significantly from both the female-skewed fed grids and male-skewed control grids (Table A2).

Reproduction, weight distributions and demographic stucture.-- Logit model tests for reproductive condition are presented in Table A3. Breeding was seasonal for both sexes, but the breeding peak for males June) was more defined than it was for females (Fig. 12). Trapping was not conducted during winter on a regular basis, but a trapping session between 10-17 November 1983 (for radiotelemetry) revealed no mice in reproductive condition. These results indicate that breeding ceased in winter despite the presence of food. A lower proportion of the sexually mature males, compared to females, was in breeding condition during any month.

Table 8. Chi-square tests on juvenile sex ratios: (a) pooled data from June 1982;
    March, May and June 1984; (b) pooled data from August 1982, 1984; October 1982,
    1983.

	(a) March-June				(b) August-October		
		Fed	Non-fed			Fed	Non-fed
Female		37	16		Female	26	24
Male		57	13		Male	28	20

$\chi^2 = 2.26$, p = 0.13 $X_2 = 0.40$, p = 0.53
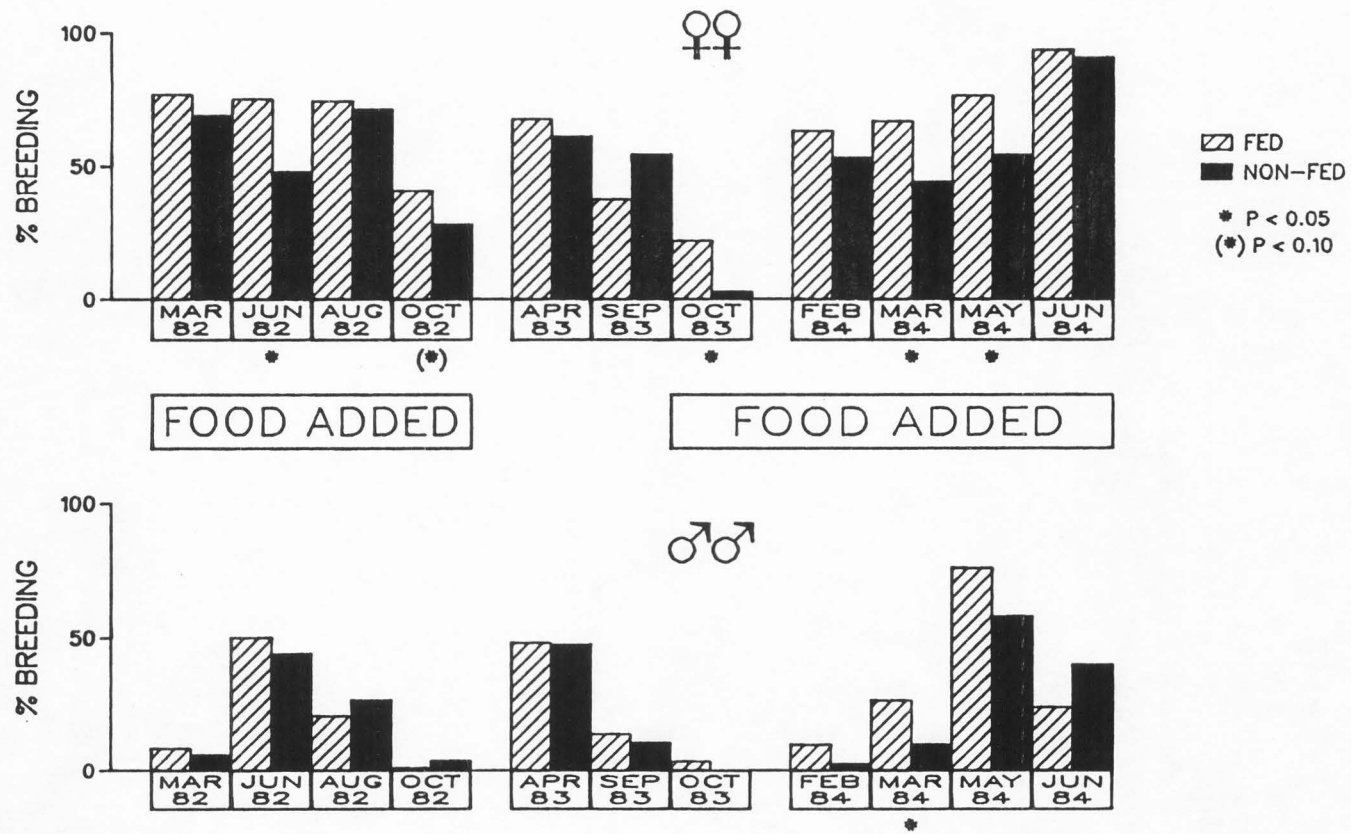
Fig. 12. Percentages of adult females and adult males in breeding condition on fed and non-fed grids. Significance levels from logit model tests between treatments.

The reproductive response of males was significantly affected by feeding only in March 1984 (Fig. 12). Females extended their breeding season into October on fed grids and more females bred earlier in spring when food was present. Although the total proportion of females in reproductive condition (perforated, pregnant or lactating) did not differ between fed and non-fed grids in March 1982, more females were pregnant on the fed grids ($X^2=4.70$, $P<.05$, Table 9), indicating that breeding did begin earlier when food was present. The physical condition of the grids outweighed the effects of food in February 1984 (Table A3). At this time grids 7, 8 and G were still snow covered, grids 1 and 2 were clear although grid 2 was still wet and muddy. Females in breeding condition were 0.0% on grids 7 and G; 17% on grid 8; 78% on grid 2; and 80% on grid 1. Detectable pregnancies occurred only on the fed grids. Females on grid 1 were perforate only (Table 9). Breeding began on grid 1 approximately 1 February (trapping was conducted 10 February) and on grid 2 approximately 20 January (calculated using a mean gestation length of 23 days [Layne 1968, Millar et al. 1979]).

Weight distributions for all mice caught on fed and non-fed grids are illustrated in Fig. 13. Mean female weights were greater, to some extent, at all times when food was present. Mean male weights were less frequently affected by feeding than were female weights. Pregnancy probably contributed to much of the weight difference. Food usually increased male weights, but in May 1984 mean weights of males were lower on fed grids due to the presence of juveniles. Adult male weights were not significantly different in May (Fig. 13). Recruitment

Table 9. Percentages of adult females in breeding condition, sub-
divided into percentages lactating, pregnant or perforated.
F = Fed grids, NF - Non-fed grids (including the shrub-
removal grid in 1983-84).

1 9 8 2

Breeding Condition	Mar.		June		Aug.		Oct.	
	F	NF	F	NF	F	NF	F	NF
Lactating	1	0	14	24	12	14	35	25
Pregnant	53	33	60	12	61	50	4	3
Perforated	24	37	1	12	2	7	2	0

1 9 8 3

	Apr.		Sept.		Oct.	
Lactating	12	16	16	38	2	0
Pregnant	44	40	9	12	17	0
Perforated	12	5	13	5	3	3

1 9 8 4

	Feb.		Mar.		May		June	
Lactating	0	0	11	2	15	14	21	23
Pregnant	20	0	39	10	57	27	71	64
Perforated	43	53	17	33	5	14	2	5
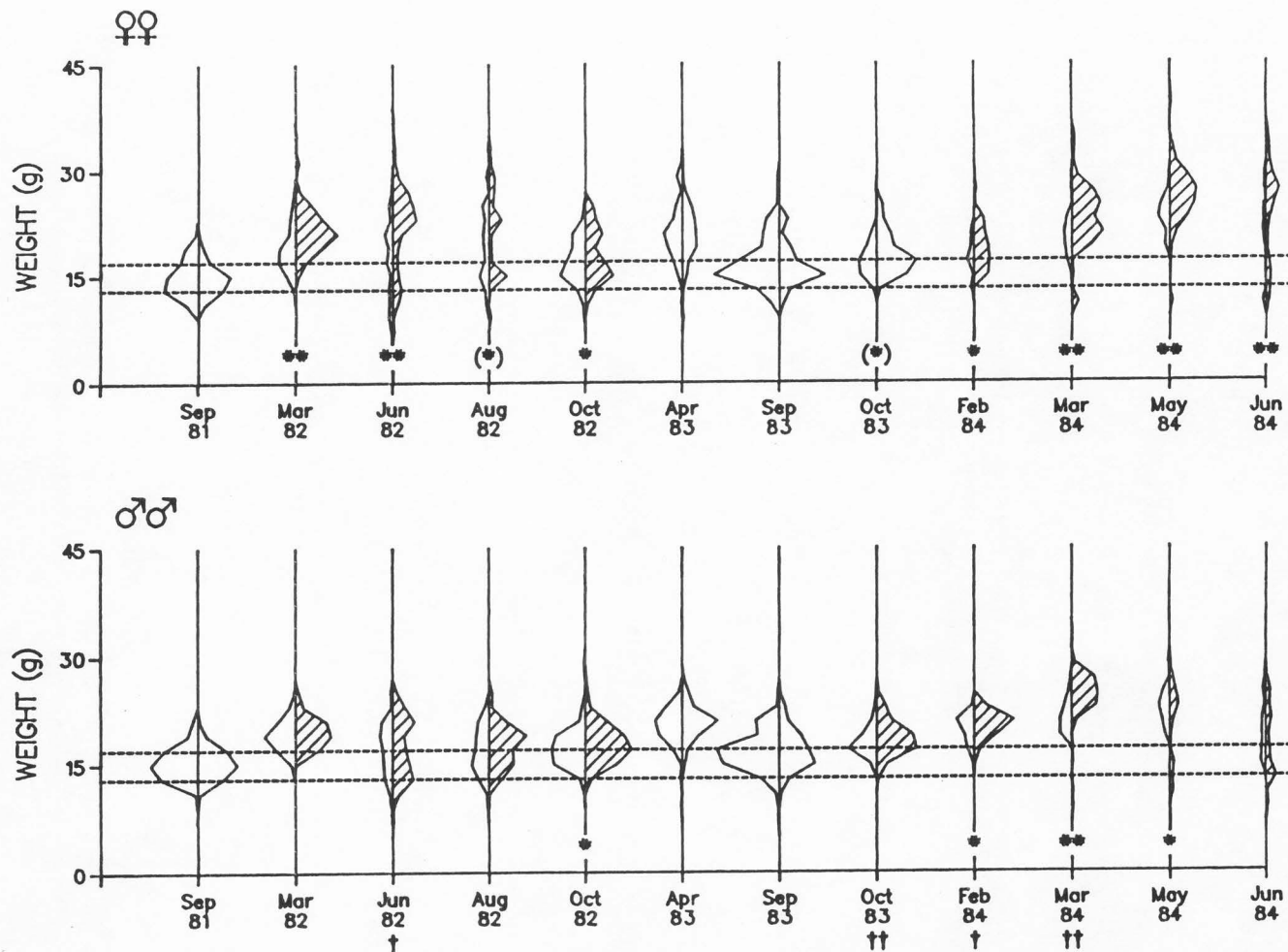
Fig. 13. Weight distributions of females and males on fed and non-fed grids, September 1981 – August 1984. Fed distributions are to the right and non-fed distributions to the left of each line. Shading indicates when food was present on the food-addition grids. Significance levels from z tests between mean weights on food-addition and control grids: ** P 0.01, * P 0.05, (*) P 0.10. Significance levels for differences in adult weights (males): † P<0.05, †† P<0.01.

of juveniles (sexes combined) was higher in early summer 1982 than in late summer/fall (June compared to August/October 1982; combined grids $X2 = 11.96$, $P<.01$). Food addition affected juvenile recruitment only in March and May 1984, when proportionately more juveniles were caught on fed grids ($X2=5.40$, $P<.05$). All juveniles were from grid 2 in March but were caught on other grids by May.

Removal of shrubs had no effect upon the proportions of adults in breeding condition, or upon weight/age structure. Breeding condition differed from the control grids only when breeding was early on grid 1 in February 1984 (Table A3). At this time the shrub-removal grid was still snow covered, only nine mice were caught and none were in reproductive condition. Weight distributions and adult male weights did not differ significantly from those on non-fed grids although adult male weights tended to be higher on the shrub-removal grid during spring 1984.

Differences in breeding intensity (% reproductive) between years may be associated with weather conditions or with population density. More adult females were reproductive in late October 1982 than in October 1983 on both fed and non-fed grids ($X2=4.92$, $P<.05$; $X2=7.60$, $P<.01$, respectively). Similarly, female breeding intensity was greater in late March 1982 than it was in March 1984 ($X2=3.46$, $P=.06$; $X2=11.90$, $P<.01$ on fed and non-fed grids respectively).

Residency and movements.--An indication of the amount of adherence to trapping grids and the amount of movement within the populations was obtained by examining indices of grid fidelity, population turnover rates on grids, and dispersal between grids. Grid fidelity (often

termed "survivorship", e.g., Taitt 1981, Taitt and Krebs 1983, Ford and Pitelka 1984, Tamarin et al. 1984, Wolff 1985a) is the percentage of animals caught during the previous trapping period which are recaught during the present trapping period, n_t/n_{t-1}, i.e., it is "survivorship" between successive trapping periods (Figs. 14, 15). Interpretation of these and the following two figures should take into account the unequal time between trapping periods.

New captures are often designated immigrants (e.g., Taitt and Krebs 1983, Ford and Pitelka 1984, Fairbairn 1977, 1978a). I prefer to use the proportions of new to total captures within trapping periods simply as indices of population turnover rates (Figs. 16, 17), and avoid attributing this unequivocally to immigration (or births) because of possible trapping biases (Section 4.3). The logit model tests associated with Figs. 14, 15 and 16, 17 are presented in Tables A4 and A5.

For females, feeding generally improved fidelity during spring, up to the point of the population crash of March 1984. Food addition did not affect fidelity in fall (Fig. 14). In March 1984 fidelity to grid 1 was as high as on the fed grids, with grid 7 lower than the rest (Z=2.955, P<.01). Turnover rates were the reciprocal of fidelity (Fig. 16). Turnover was reduced by food addition during the spring of 1982, although it was equivalent to that of the control grids during the severe 1984 spring decline. The reaction of males to feeding was the converse of females. Neither fidelity (Fig. 15) nor turnover rates (Fig. 17) were affected by feeding in spring. Male fidelity was improved by feeding during fall (1982: the high % of new captures and
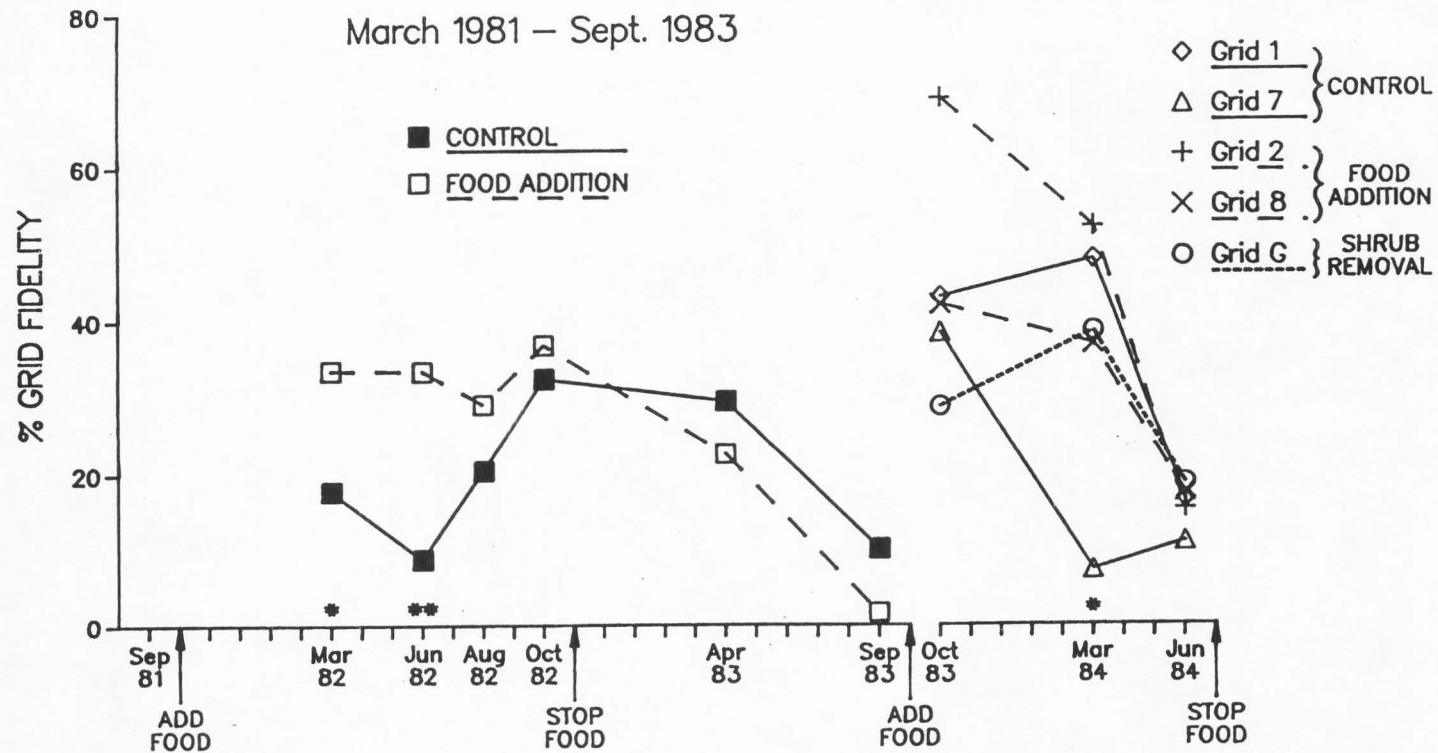
Fig. 14. Grid fidelity of adult and subadult females on pooled fed and non-fed grids for September 1981 - September 1983; and for separate food-addition and control grids and the shrub-removal grid from September 1983 - August 1984. Significance levels from logit model tests between food-addition and control grids: ** P<0.01, * P<0.05.
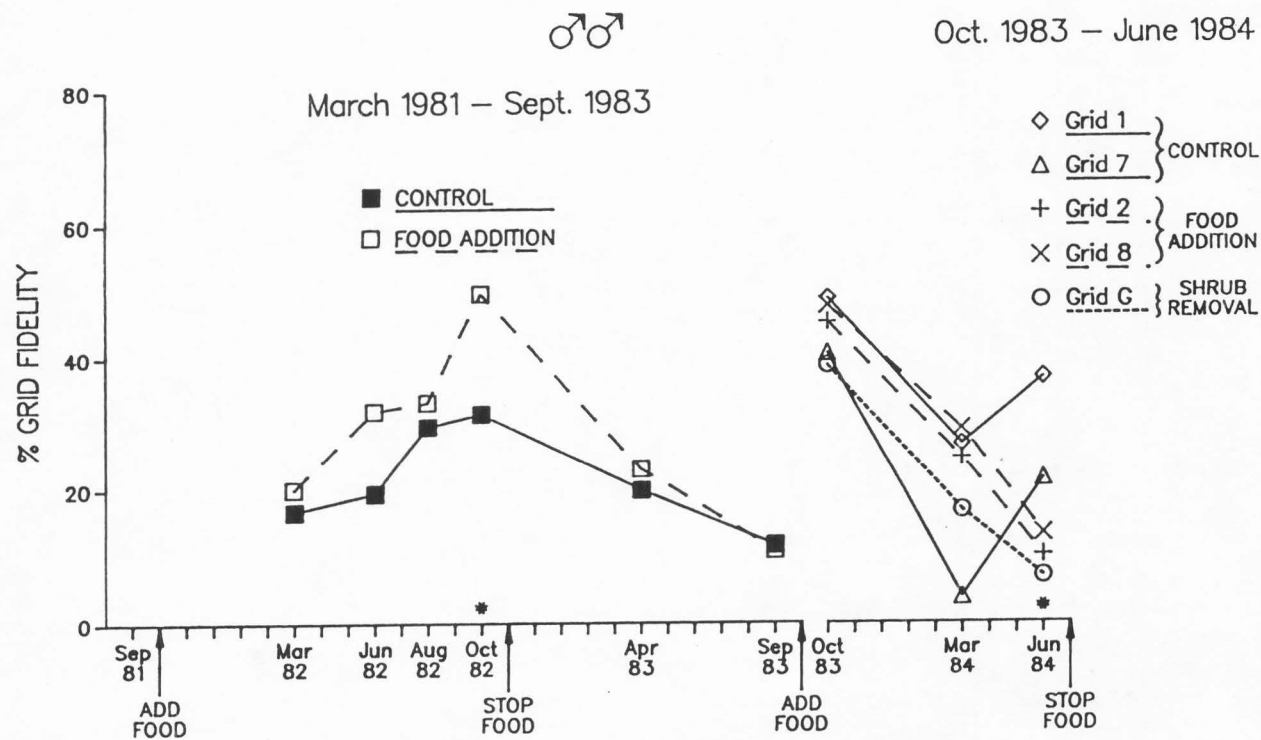
Fig. 15. Grid fidelity of adult and subadult males on pooled fed and non-fed grids for September 1981 – September 1983; and for separate food-addition and control grids and the shrub-removal grid from September 1983 – August 1984. Significance levels from logit model tests between food-addition and control grids: ** P<0.01, * P <0.05.
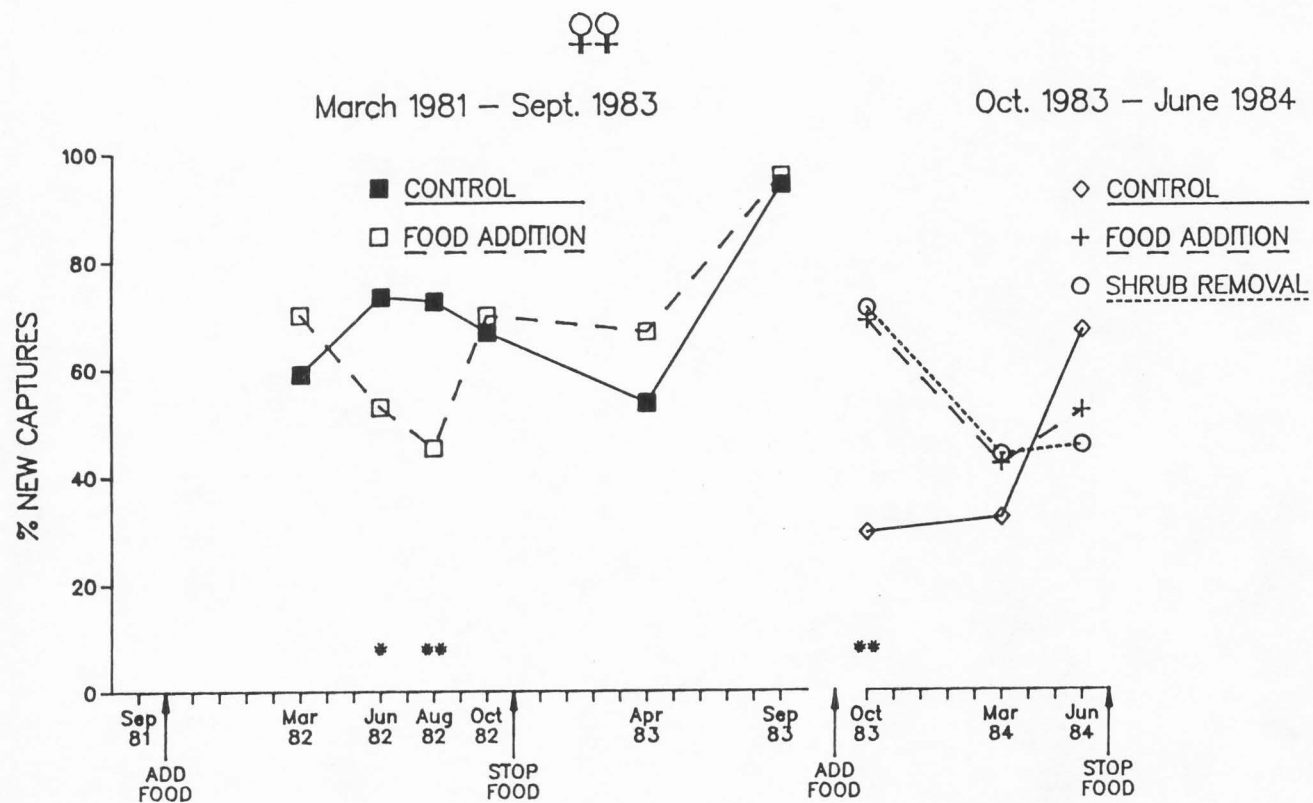
Fig. 16. Grid turnover rates (percent new captures) of adult and subadult females on control and food-addition grids and the shrub-removal grid. Significance levels from logit model tests between food-addition and control grids: ** P<0.01, * P<0.05.
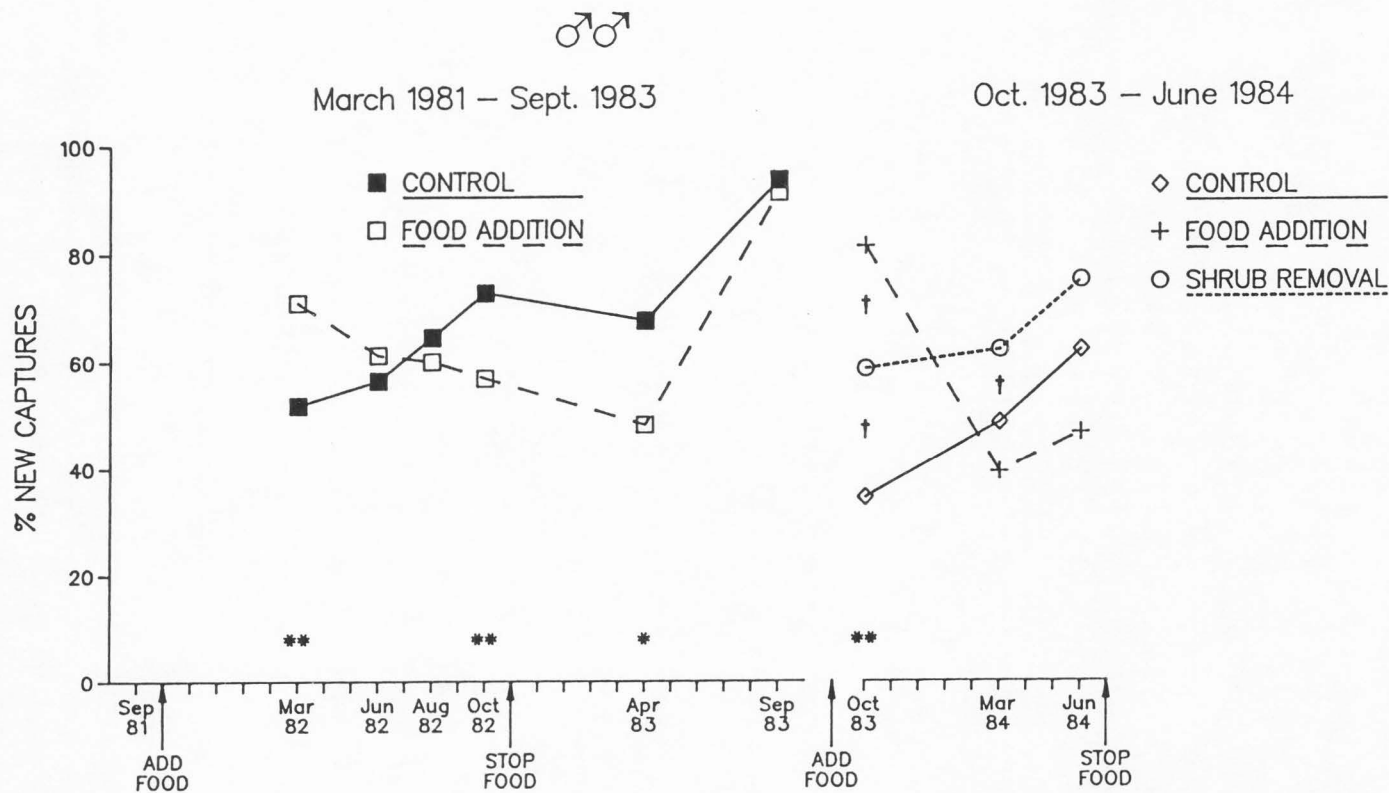
Fig. 17. Grid turnover rates (percent new captures) of adult and subadult males on control and food-addition grids and the shrub-removal grid. Significance levels from logit model tests between food-addition and control grids: ** P<0.01, * P<0.05; shrub-removal versus food-addition or control † P<0.05.

variable fidelity in October 1983 for both sexes was due to an influx of mice following initiation of feeding in September 1983). Greater adherence to grid 1 than to grid 7 was also shown by males (grid 7 vs. 1,2,8: Z=2.526, P<.05). On the shrub-removal grid female fidelity was as high in March 1984 as on the fed grids and grid 1 (Fig. 14), and was significantly higher than on grid 7 (Z=2.513, P<.05) despite the absence of mice on the grid during winter. Similarly for males (Fig. 15) fidelity generally paralleled that on fed grids; although it was intermediate between the fed grids and grid 7 in March 1984 (Table A4).

Sample sizes of juveniles were sufficient for comparisons of fidelity only between summer (June - August) and fall (August - October) 1982 (Table 10). Logit model tests indicated no differences in fidelity due to sex or feeding (although sample sizes when divided by sex and grid were small). Analysis of the combined sample indicated that juveniles had greater fidelity to the trapping grids in fall than in summer (Table 10).

Fidelity for adults and subadults was compared between fall and spring (overwinter) and from spring to fall (oversummer), Table 11. Results of the logit model tests are provided in Table 12. As indicated from the previous serial analysis (Figs. 14, 15), only female overwinter (September to March) fidelity was significantly increased when food was provided (Table 11). Feeding made no difference to oversummer fidelity. Overwinter fidelity (average 22.3%) was greater than oversummer fidelity (average 7.5%) for both sexes (P1, P2, P3 vs. P4, P5 - Table 12). Overwinter fidelity (6 months) of mice trapped in October was greater than that of mice trapped in September (P2 vs. P1,

Table 10. Grid fidelity of juveniles in summer and fall of 1982 on combined fed and combined non-fed grids. Significance levels: ** = 0.01; * = 0.05.

Time period	Grid	Number captured				% Fidelity		Sexes & Grids Combined
		M	F	M	F	M	F	
Jun.-Aug. 1982	Fed	31	14	11	2	35.5	11.1	26.5
	Non-fed	12	11	2	3	16.7	27.3	
Aug.-Oct. 1982	Fed	15	3	10	1	66.7	66.7	54.1
	Non-fed	12	7	5	4	41.7	42.9	

Results of logit model tests: (Saturated model = G,S,D,GD,GS,DS,GDS)

Parameters omitted	L.R. Chi square	P-level
All 3-way & 2-way interactions	2.723	0.605

Contrast	Z-value	Sig.-level
Sex	0.656	NS
Date	2.855	**
Grid	1.316	NS

Parameters omitted	L.R. Chi square	P-level
All interactions, sex, grid	5.359	0.499

Contrast	Z-value	Sig. level
Date	2.758	**

Table 11. Overwinter and oversummer grid fidelity for adults and sub-
adults on combined fed and combined non-fed grids 1981-1984, and
on the shrub-cleared grid for the winter of 1983-84. Significant
differences between sexes and grids within periods are indicated.
Significance levels: * = 0.05; (*) = 0.01. (Z values from logit
model tests.)

| Time Period | | | | Overwinter fidelity | | | | | |
Period #	# Months	Months	Grids	#-fall M	F	#-spring M	F	% grid fidelity M	F
1	6	9/1981-3/1982	Fed	109	89	22	30	20.2 *	33.7 *
		(food present)	Non-fed	132	107	22	19	16.7	17.8
2	6	10/1982-4/1983	Fed	135	88	31	20	23.0	22.7
		(no food)	Non-fed	96	74	19	22	19.8	29.7
3	6	9/1983-3/1984	Fed	75	67	16	24	21.3 (*)	35.8 *
		(food present)	Non-fed	78	90	12	17	15.4	18.9 *
			Shrub-removal	31	31	9	10	29.0	32.3

| | | | | Oversummer fidelity | | | | | |
				# - Spring M	F	# - fall M	F	M	F
4	7	3/1982-10/1982	Fed	97	131	7	10	7.2	7.6
		(food present)	Non-fed	72	56	4	2	5.6	3.6
5	5	4/1983-9/1983	Fed	74	60	8	1	10.8 (*)	1.7 (*)
		(no food)	Non-fed	67	59	8	6	11.6	10.2

Table 12. Results of logit model tests for overwinter and oversummer grid fidelity (Adults and Subadults). Replicate grids within treatments are combined. Significance levels: ** = 0.01; * = 0.05; (*) = 0.10.

Contrast	MALES Combined Fed & Non-fed grids		FEMALES Fed grids		Non-fed grids	
	Z value	Sig. level	Z value	Sig. level	Z value	Sig. level
Periods						
P1 vs. P3	0.011	NS	0.275	NS	0.205	NS
P2 vs. P1,P3	3.193	**	1.946	(*)	3.668	**
P4 vs. P5	1.487	NS	1.494	NS	1.331	NS
P1,P2,P3 vs. P4,P5	4.064	**	4.477	**	3.264	**
Grids						
Fed vs. Non-fed	1.171	NS	1.971 * (differs by period, see Table 16)			

(+) Simplest models which fit data: (Saturated = G,P,GP)

Sex	Parameters omitted from model	L.R. Chi square	P-level
Females	Grid x Period	14.837	0.005 **
	Grid, G x P	18.756	0.002 **
	Period, G x P	73.11	0.000 **
	(+) none	0.0	1.0
Males	Grid x Period	0.5907	0.964
	(+) Grid, G x P	1.969	0.853
	Period, G x P	23.86	0.002 **

P3 - Table 12). This was possibly because mice were moving through the population to a greater extent in September, but were adhering to the grid more in October. Extensive early fall movements would explain the decline in $\hat{N}$ which occurred on non-fed grids between September and October 1983 (Fig. 10). By contrast, on the shrub-removal grid males trapped in September had higher overwinter fidelity (29%) than those newly-caught in October (5.6%) $X^2 = 3.86$, P<.05. Grid turnover rates of both sexes were also high during October compared to control grids (Figs. 16, 17), and turnover rates were high for males in March (Fig. 17). These observations are consistent with resident mice leaving the grid during winter, but returning in spring. Capture histories indicate that the high fidelity and high turnover rates on this grid were due to a base population of residents with a highly vagile population of non-residents, especially males. Most of the male recaptures in March, May, and June were of animals originally caught in September ($X^2=9.55$, P=.002). Few (two) of the new captures from October and March were recaptured.

Indices of dispersal between adjacent trapping grids (Table 13) indicate that immigration contributed to the initial increase in population size following food addition. During March 1982 and October 1983 all movements were from non-fed to the adjacent fed grids. By contrast, in April 1983 after feeding had ceased the movement was in the opposite direction, away from the fed grids. Movements away from fed grids also occurred in late summer (August 1982). During the 1984 spring decline the rate of dispersal onto the food-addition grids declined but did not increase on the control grids. In combination

Table 13. Indices of dispersal onto food-addition grids (grids 2,8), control grids (1,7) and
the shrub-removal grid (G). Numbers are the percentage of grid recaptures which originated
from the adjacent grid.

Grid	Inter-grid distance	Mar. 82	June 82	Aug. 82	Oct. 82	Apr. 83	Oct. 83	Feb. 84	Mar. 84	May 84	June 84	Aug. 84
2 - from grid 1	180 m	25	28	6	4	0	8	16	10	7	4	-
8 - from grid 7	272 m	0	0	0	0	0	5	19	12	6	4	0
1 - from grid 2	180 m	0	1/2*	13	0	11	0	0	0	0	0	-
7 - from grid 8	272 m	0	0	10	0	25	0	7	0	0	0	0
G - from grid 7	593 m	-	-	-	-	-	0	0	0	7	10	-

* Only two recaptures, one from grid 2. Elsewhere, sample size of total recaptures was between 10-26.

with the severity of injuries (next section), this suggests that the fate of many excluded individuals during this decline was death rather than dispersal.

Injuries.--Injuries were recorded after September 1983. Wounding coincided with the onset of breeding; in March and May 1984 a high proportion of the adults of both sexes were severely wounded (Fig. 18), males more so than females (results of the logit model tests are presented in Table A6). None of the subadults (N=45) trapped in February, March or May were injured. The adult injury rate did not differ significantly among the five grids until February when approximately 10% of both sexes on fed grids were wounded. By March, 53% of males and 24% of females on grid 1 as well as on the fed grids (2 and 8) carried injuries, and this rose to 60% of the adult males by May. Females on grid 2 had a higher level of wounding in March and May than on grid 8 (Fig. 18, $X^2=4.58$, P<.05 for the two months combined), coincident with earlier breeding and a higher population size. (These differences were not significant for the individual months from the logit analysis due to small sample size). In June, following the decline in numbers on fed grids, the level of wounding of the remaining animals did not differ from grid 7 or the shrub-removal grid; both of these sustained very low injury rates throughout the entire period.

High rates of injury were not observed between September 1981 and April 1983; had injuries been present at levels comparable to 1984 they could hardly have escaped notice. The extreme injuries in March and May 1984 probably led to death of many animals, either through sepsis of open wounds (many of which were extremely putrid), or by
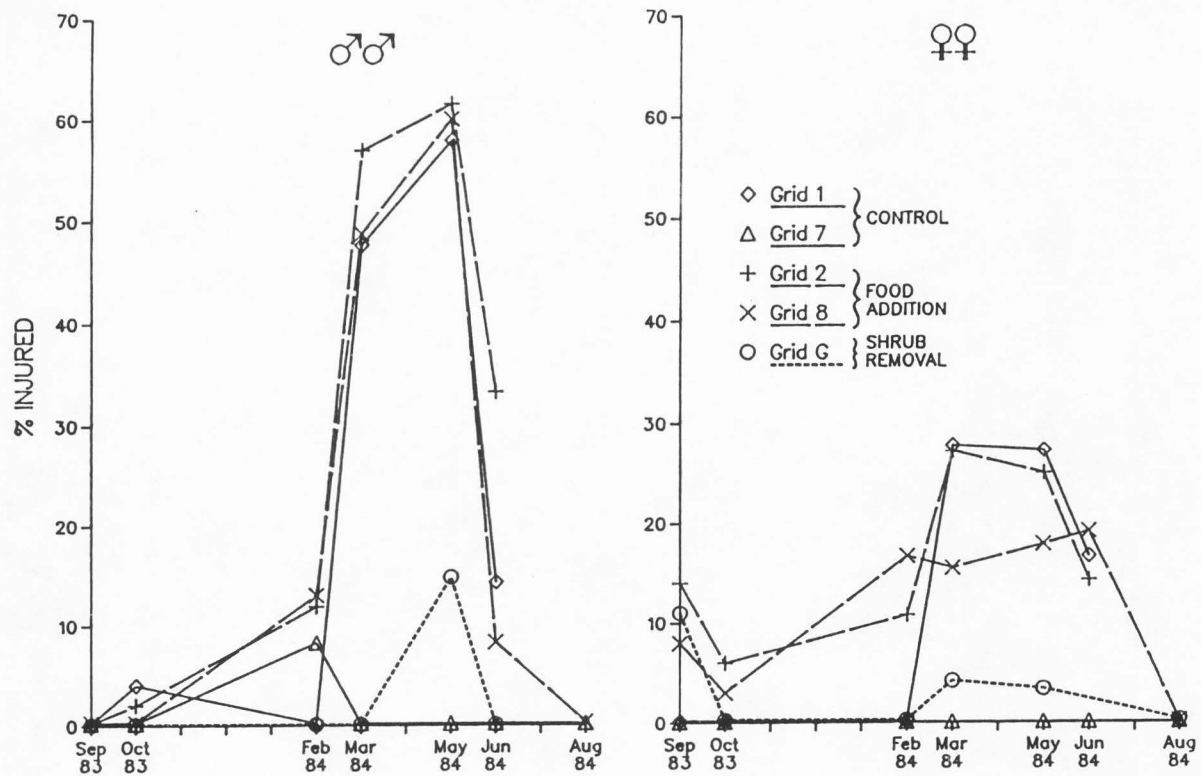
Fig. 18.   Percentages of adult males and adult females with severe injuries, September 1983 –
August 1984.

susceptibility to predation. A number of animals died in the traps apparently too weakened to withstand overnight detainment. Injuries included complete removal of tails, legs and feet (both pes and manus), ulcerated faces, lost eyes and ears, and ulcerated wounds on the rump, neck and shoulders. Several females had ulcerated stomachs, and one removed dead from a trap burst open and appeared to be rotting from within. The high levels of stress undoubtedly manifest with these outward signs were likely associated with the hypothalamo-pituitary-adrenocortical syndrome (Christian 1963, 1978; Christian and Davis 1964, Davis 1978) leading to breakdown of the immune system. Suscepti-bilty to infection was clearly high and the intra-peritoneal condition in females may have resulted from ulcers or inability to reabsorb embryos.

Chi-square tests were used to determine which of the adult animals were suffering most injuries when the social strife began in March 1984 on grids 1, 2 and 8. Animals were categorized according to breeding condition, overwinter residency (recapture or new capture since the last complete trapping period in October 1983) and weight (greater or less than the median adult weight, 23.5 g). For males (Table 14) the breeding (scrotal testes and/or perianal pouches), heavy weight, over-wintered residents carried most injuries ($X^2=9.45$, P<.01; $X^2=5.27$, P<.05, $X^2=9.60$, P<.01 repectively). In contrast, more injuries were inflicted upon the non-breeding females ($X^2=7.00$, P<.01) with a ten-dency towards lighter weight ($X^2=2.83$, P=.09). Breeding condition was associated with heavier weight in both sexes ($X^2=33.50$, $X^2=48.93$ P<.01 for males and females, respectively), but overwinter residency was

Table 14. The percentage of adults injured in March 1984 on grids 1, 2 and 8, classified according to breeding condition, weight and over-winter residency. Sample sizes given in parenthesis. Signifcance levels by Chi-square tests: ** = 0.01, * = 0.05, (*) = 0.10.

Males			Females		
Breeding		Non-breeding	Breeding		Non-breeding
72.5 (40)	**	42.0 (69)	16.5 (103)	**	35.2 (54)
> 23.5 g		< 23.5 g	> 23.5 g		< 23.5 g
71.4 (28)	*	46.3 (82)	17.1 (81)	(*)	28.4 (76)
Resident		New capture	Resident		New capture
64.7 (68)	**	34.1 (41)	23.1 (91)	NS	22.7 (66)

associated with neither weight nor breeding condition. A higher pro-
portion of those males which had perianal pouches but regressed testes
were injured than males who had descended testes (χ^2=3.79, P=.051).

Distances moved on the trapping grids.--The addition of food
affected distance moved between successive captures within capture
periods (Fig. 19). Mice moved shorter distances between traps on the
fed grids, at all times when food was present, except in October 1982.
On non-fed grids males moved greater distances than females during
three of the trapping periods. Sexes did not differ on fed grids
except during April 1983, when food was absent; although the trend was
for greater movement by males in all months. Distances moved on the
shrub-removal grid were intermediate between and not significantly
different from fed and non-fed grids.

Intergrid differences.-- The strong differences between grids 1
and 7 (controls), and between grids 2 and 8 (food-addition grids) in
February and March 1984 were due to differences in slope and aspect
between the grid sites. Grid 1 (on a relatively steep, south-facing
slope) was particularly well situated for early spring snowmelt (e.g.,
in late January 1984 it was an island of dry habitat when snow covered
the surrounding areas). Hence the early breeding, high fidelity and
high injury rates; all equivalent to those produced on the food-
addition grids. Sex ratios and population sizes were not affected to
the same degree, although $\hat{N}$ was larger than on grid 7. Similarly, in
the wet spring of 1983 when snow storms continued through March,
breeding (by females) was elevated on grid 1 (Table A3), and popula-
tion sizes were larger than on any of the other non-fed grids. In the
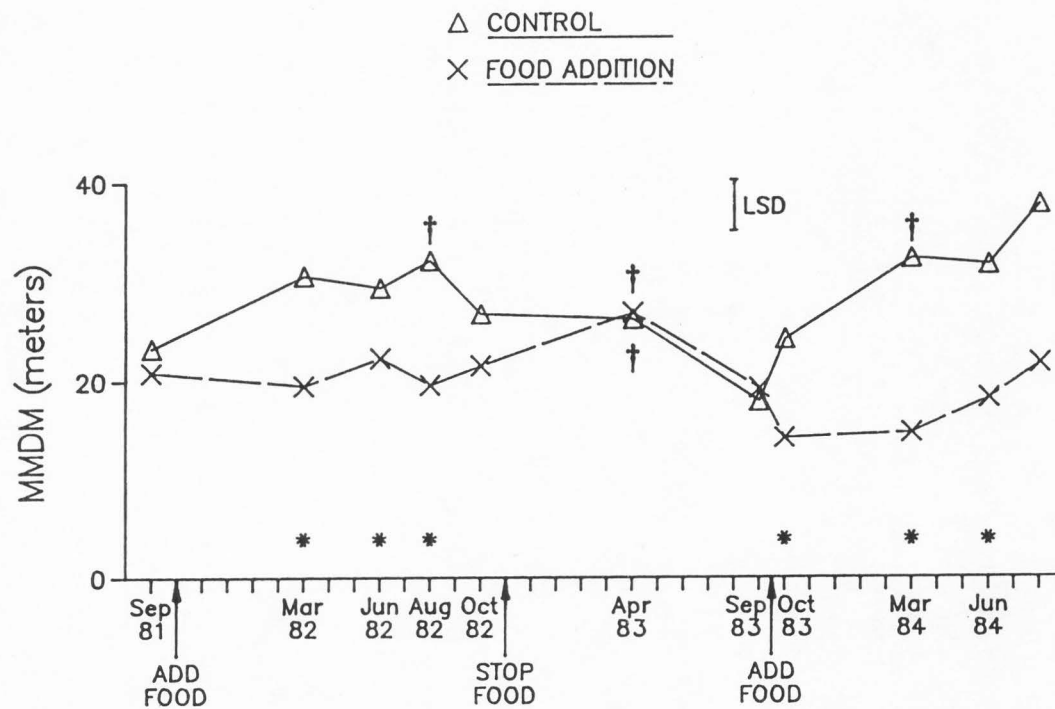
Fig. 19. Mean maximum distances moved (MMDM) between successive trap captures on fed and non-fed grids. Significance levels from analysis of variance: fed versus non-fed * P<0.05; female versus male   P<0.05.

spring of 1982 (March, June), which followed a relatively mild winter with light snowcover and early snowmelt, no significant differences were found among all five non-fed grids. These results suggest that the responses obtained on grid 7 in 1984, rather than on grid 1, were representative of the general control situation. They also demonstrate that environmental heterogeneity can lead to marked differences in population parameters over a small geographical area.

Similar differences in responses occurred between the two food-addition grids in 1984. Early snowmelt on grid 2 coincided with higher female fidelity, $\hat{N}$'s, female injury rates, and earlier onset of breeding. In contrast, during March 1982 $\hat{N}$ was greater on grid 8, as was breeding for females (Table A3) and grid fidelity (combined sexes, $X^2 = 7.21$, $P < .01$). No 1982 record was kept of localized snow conditions, however, these results suggest that the quality of localized habitats can vary annually.

Snowtracking.--Counts of tracks in snow revealed differences in mouse activity levels between the three treatment grids on which radio telemetry was conducted, and between dates (Tables 15 and 16). The only non-significant difference was between the food-addition and control grids in February. Most activity occurred on the fed grid, followed by the control and shrub-removal grids (Table 15). Activity was highest in November, particularly on the food-addition grid (probably due to seed caching), decreased in December and increased in February. The distributions of activity across the grids were compared by chi-square tests on the number of tracks occurring per grid square and are illustrated in Fig. 20. Tracks occurred only on the outer three grid

Table 15. The total number of mouse tracks recorded on the three radio-
telemetry grids, winter 1983-84.

	Month		
Grid	November	December	February
Shrub-removal	23	0	7
Control	55	8	50
Food addition	220	27	41

Table 16. Results of loglinear model tests (z values) for the number
of mouse tracks on the three radiotelemetry treatment grids,
winter 1983-84. Significance levels: ** = 0.01.

	Month		
Comparison	November	December	February
Control vs. Shrub-removal	3.473 **	2.084 **	4.871 **
Fed vs. Shrub-removal	10.330 **	3.274 **	4.299 **
Control vs. Fed	9.176 **	2.962 **	0.932 NS

† Model = G,D,GD

Date comparisons (pooled grids)	Z-value
November vs. December	6.427 **
December vs. February	3.679 **
November vs. February	5.917 **
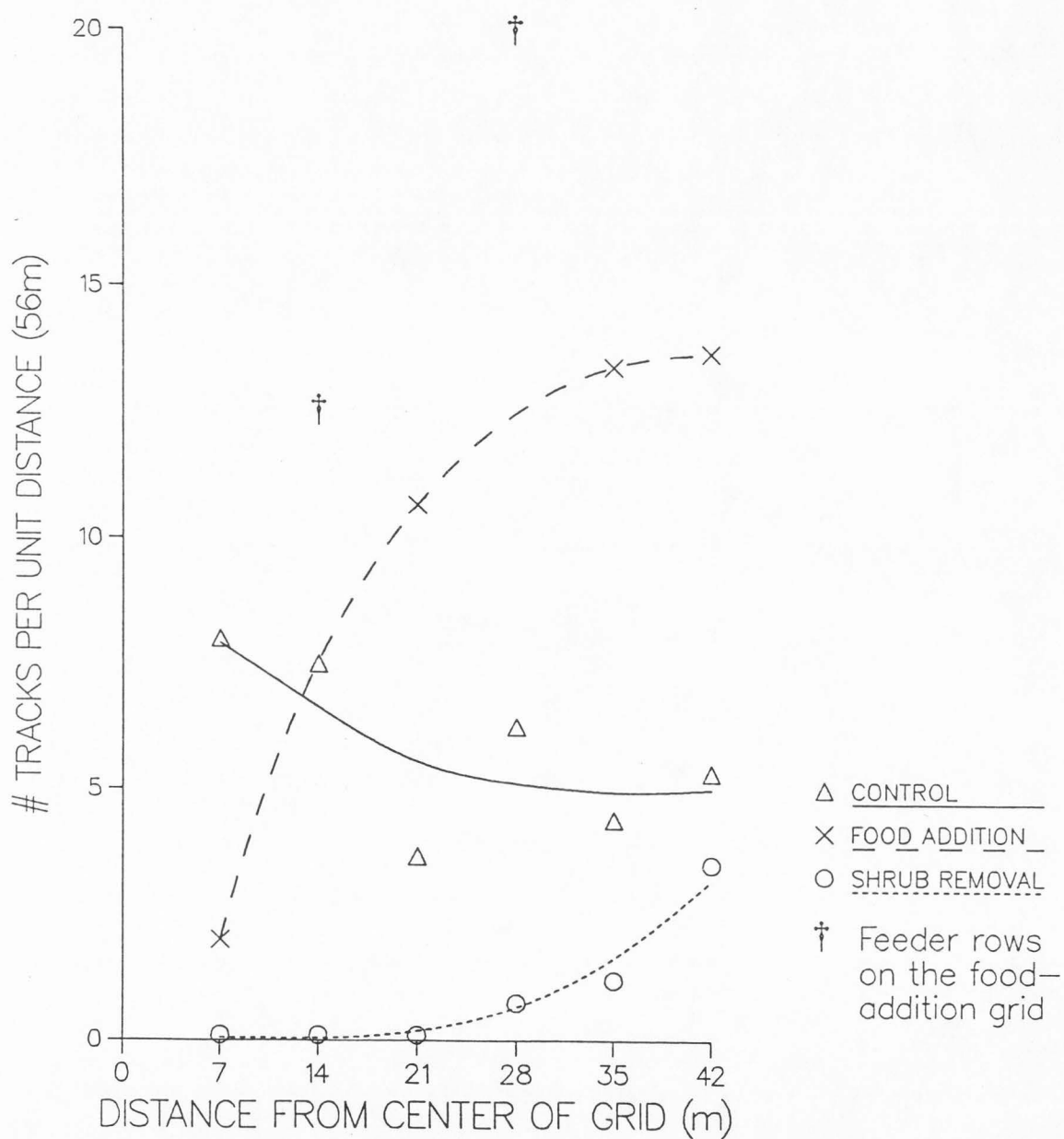
Fig. 20. The number of mouse tracks in snow as a function of
distance from the edge of each grid, months combined.

squares of the shrub-removal grid in November and the outer two squares in February. None were evident in December. These tracks originated from the shrubs bordering the grid. Activity was greatest towards the center of the control grid, possibly because it was situated on a low rise with snow depth increasing towards the perimeter. On the food-addition grid, activity was highest on the feeder rows (unconnected points on Fig. 20) and towards the edge. All distributions were significantly different (G vs. C X^2=21.92, G vs. F X^2=24.02, C vs. F X^2=16.65, P<.01).

4.2 Deermouse Individual Activity Patterns and Use of Space

Home range sizes for each radiotracked mouse, with grid means for winter (November/February) and summer (May/June/August), are detailed in Table A7. Two exceptions should be noted. Mouse 5008 on the food-addition grid (summer) was not included in the calculation of the mean because of insufficient locations (it was eaten by a weasel four days after being released with a transmitter. Secondly, the core area (0.6 ha) rather than the 75% harmonic mean contour (1.3 ha), was used for mouse 4401 on the control grid. Its large 75% area was due to two sets of outlier points, the core area was explored on most nights. A summary of the mean home range sizes for each grid is provided in Table 17. The analysis of variance for differences in home range size between grids, season and sex is presented in Table 18. Home ranges represented by seventy-five percent harmonic mean contours, centers of activity and nest-site locations for all mice tracked on each grid for winter and summer are illustrated in Figs. 21 - 26. Females and males

Table 17. Mean home range size estimates (75% harmonic mean) of radiotracked mice in summer and winter (X ± SD).

| Grid | Home range size (m^2) | |
	Winter	Summer
Food-addition	453 ± 441	2661 ± 1048
Control	1987 ± 1282	3147 ± 1584
Shrub-removal	1988 ± 940	7010 ± 2956

84

Table 18. Analysis of variance for home range size (75% harmonic mean) by grid, season, and sex. Significance levels: ** = 0.01; * = 0.05.

Source of Variation	df	F-ratio	Probability	Significance level
Grid (G)	2	7.93	0.002	**
Season (S)	1	24.47	0.000	**
Sex (A)	1	1.92	0.178	NS
GS	2	2.68	0.087	NS
GA	2	0.13	0.880	NS
SA	1	1.48	0.24	NS
GSA	2	0.41	0.67	NS
Grid (Winter)	2	6.59	0.010	**
Control vs. Shrub-removal	1	0.00	0.999	NS
Fed vs. Control/Shrub-removal	1	13.10	0.003	**
Grid (Summer)	2	9.33	0.002	*
Fed vs. Control	1	0.19	0.668	NS
Fed/Control vs. Shrub-removal	1	18.66	0.000	**
Season (Grid)				
Fed - Winter vs. Summer	1	29.26	0.000	**
Control - Winter vs. Summer	1	1.87	0.199	NS
Shrub-removal - Winter vs. Summer	1	10.49	0.010	*

CONTROL

WINTER

1987 ± 1282
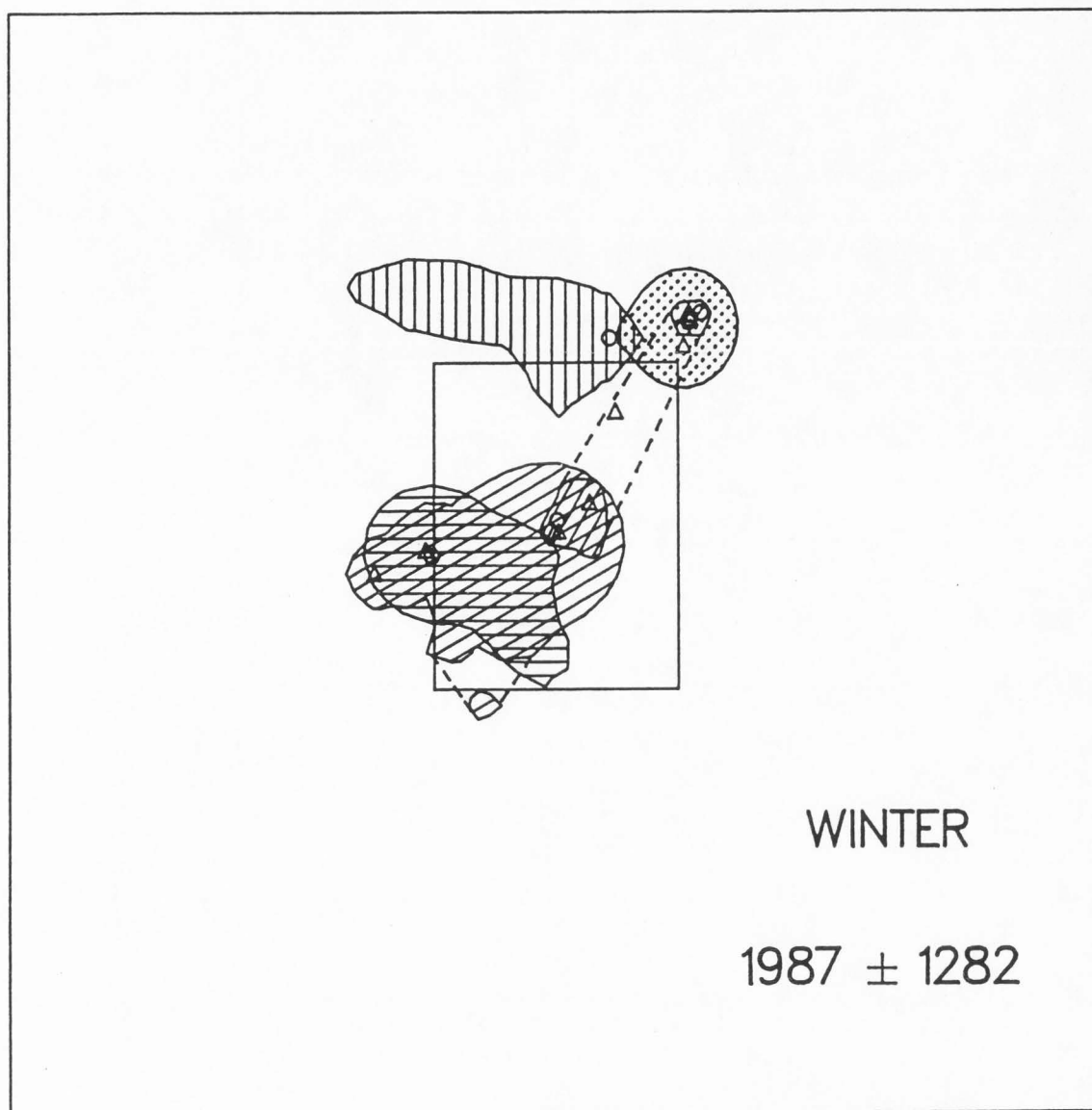
△ nest–site   ▦ female home range

○ center of activity   ▨ male home range

Fig. 21. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the control grid in winter. Mean home range size (m^2) ± one standard deviation provided.

CONTROL
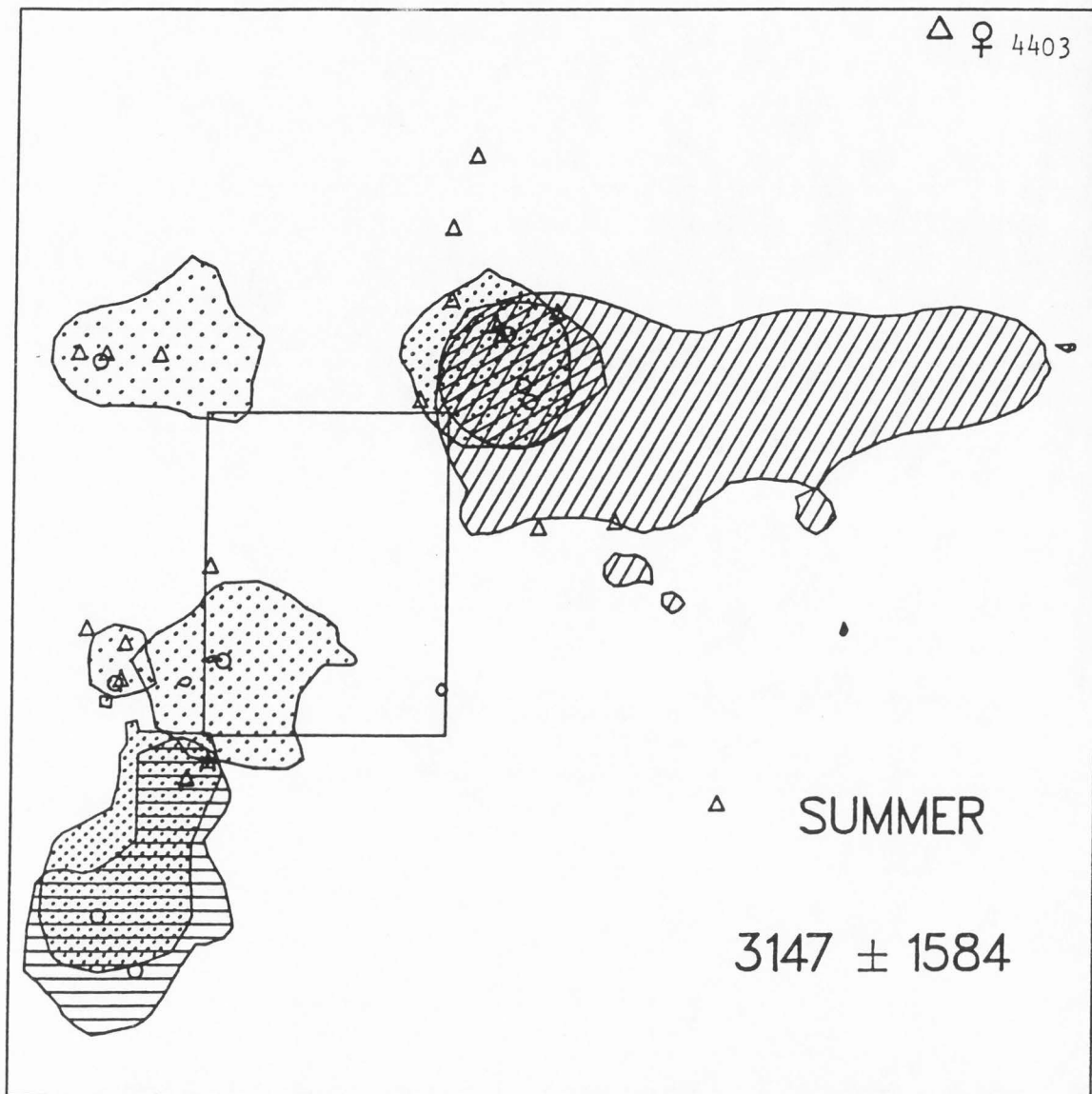
Fig. 22. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the control grid in summer. Mean home range size (m2) ± one standard deviation provided.

FOOD ADDITION

WINTER

453 ± 441
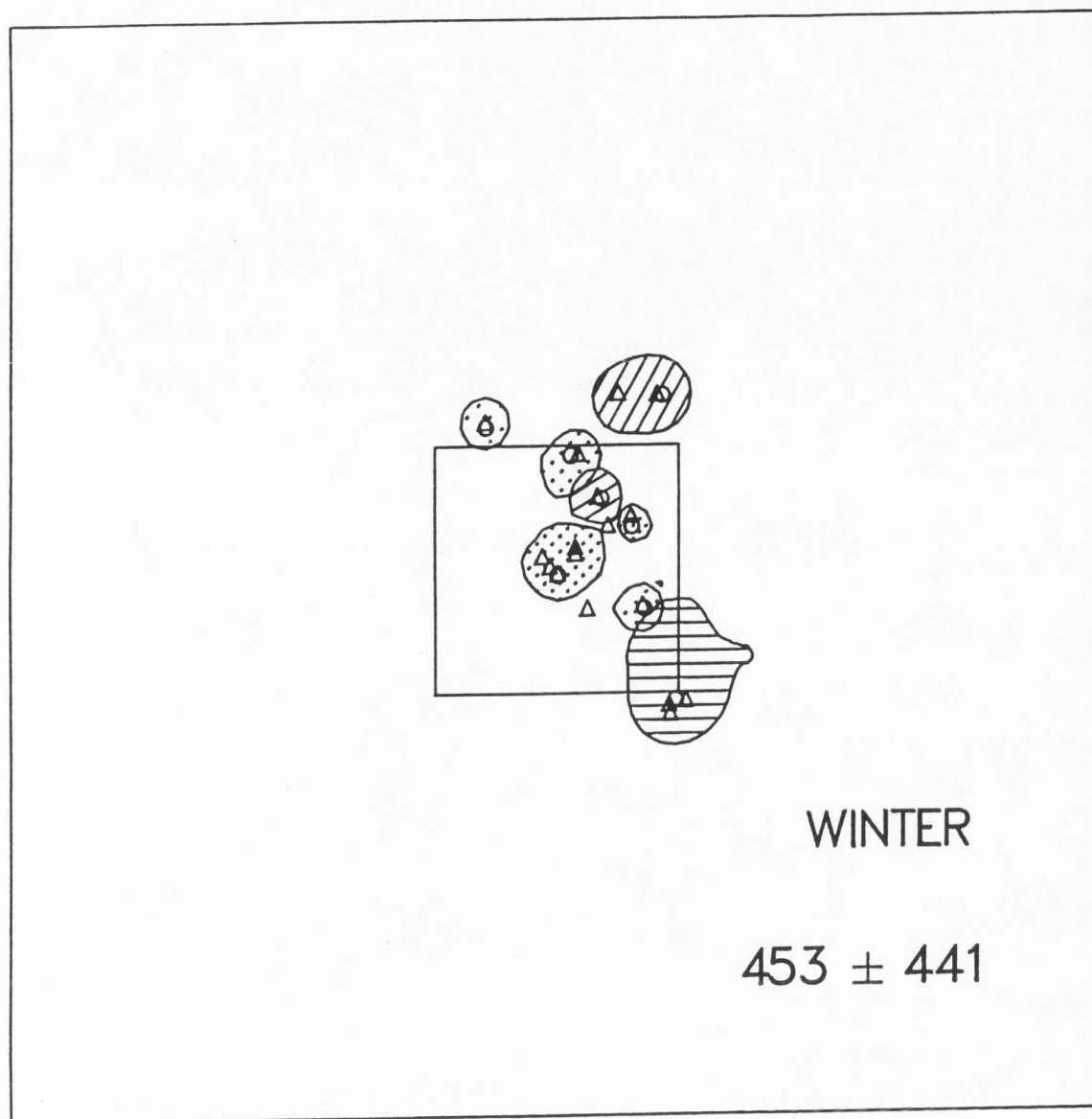
△ nest—site

◯ center of activity

▦ female home range

▨ male home range

Fig. 23. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the food-addition grid in winter. Mean home range size (m2) ± one standard deviation provided.

FOOD ADDITION

88
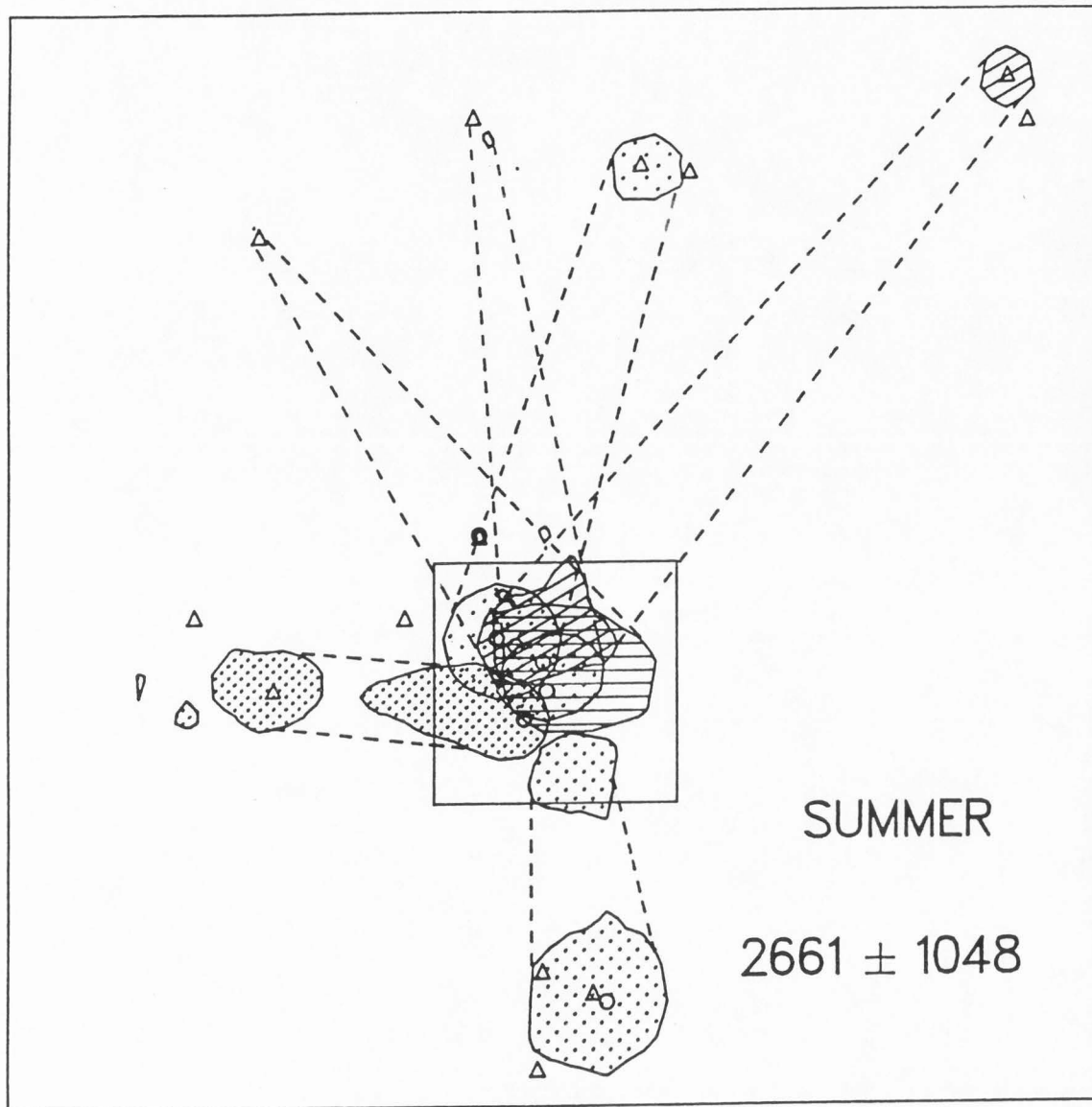
Fig. 24. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the food-addition grid in summer. Mean home range size (m2) ± one standard deviation provided.

SHRUB REMOVAL

WINTER

1988 ± 940
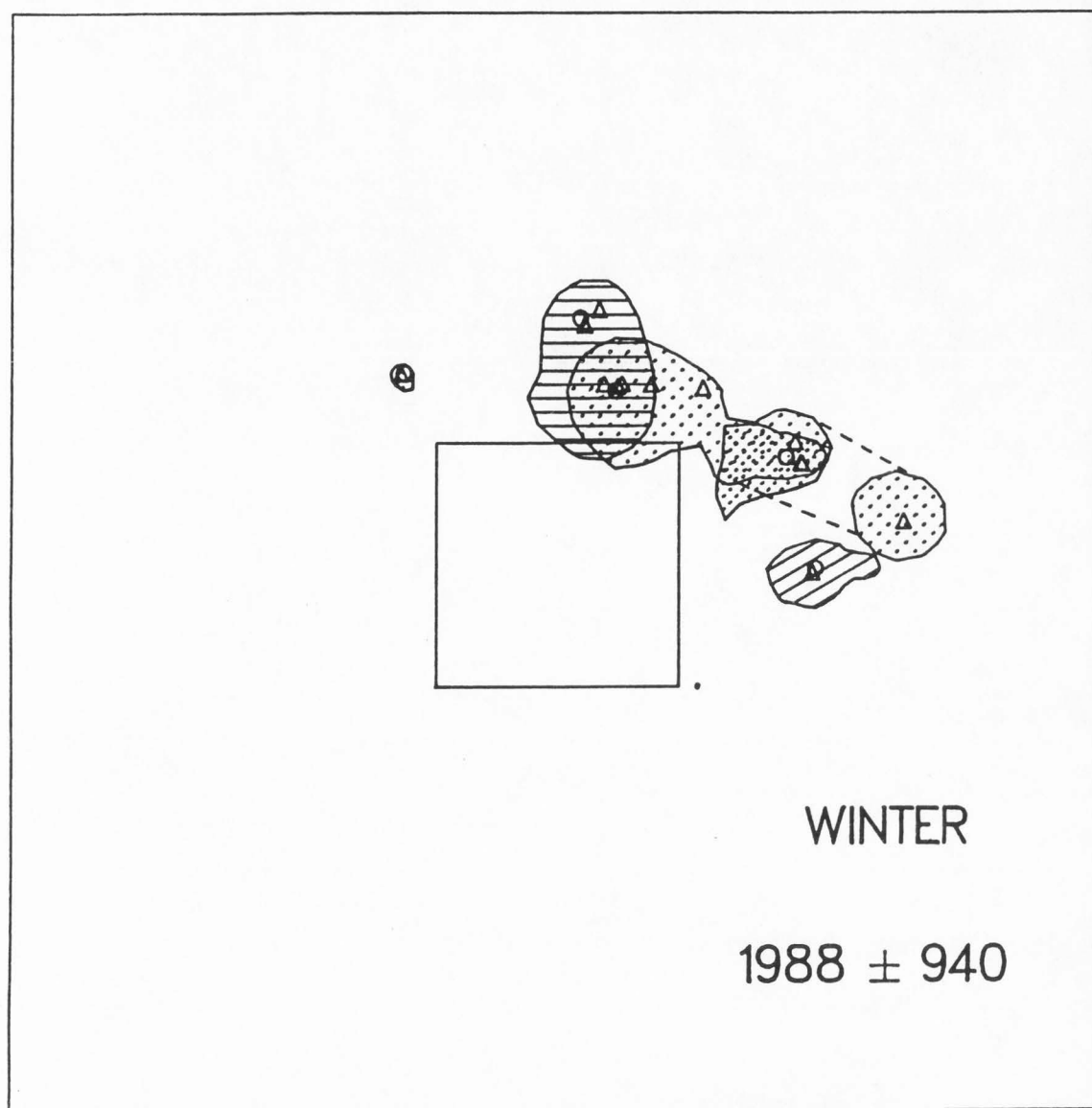
△ nest—site   ▦ female home range

○ center of activity   ▨ male home range

Fig. 25. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the shrub-removal grid in winter. Mean home range size (m2) ± one standard deviation provided.

SHRUB REMOVAL

SUMMER

7010 ± 2956
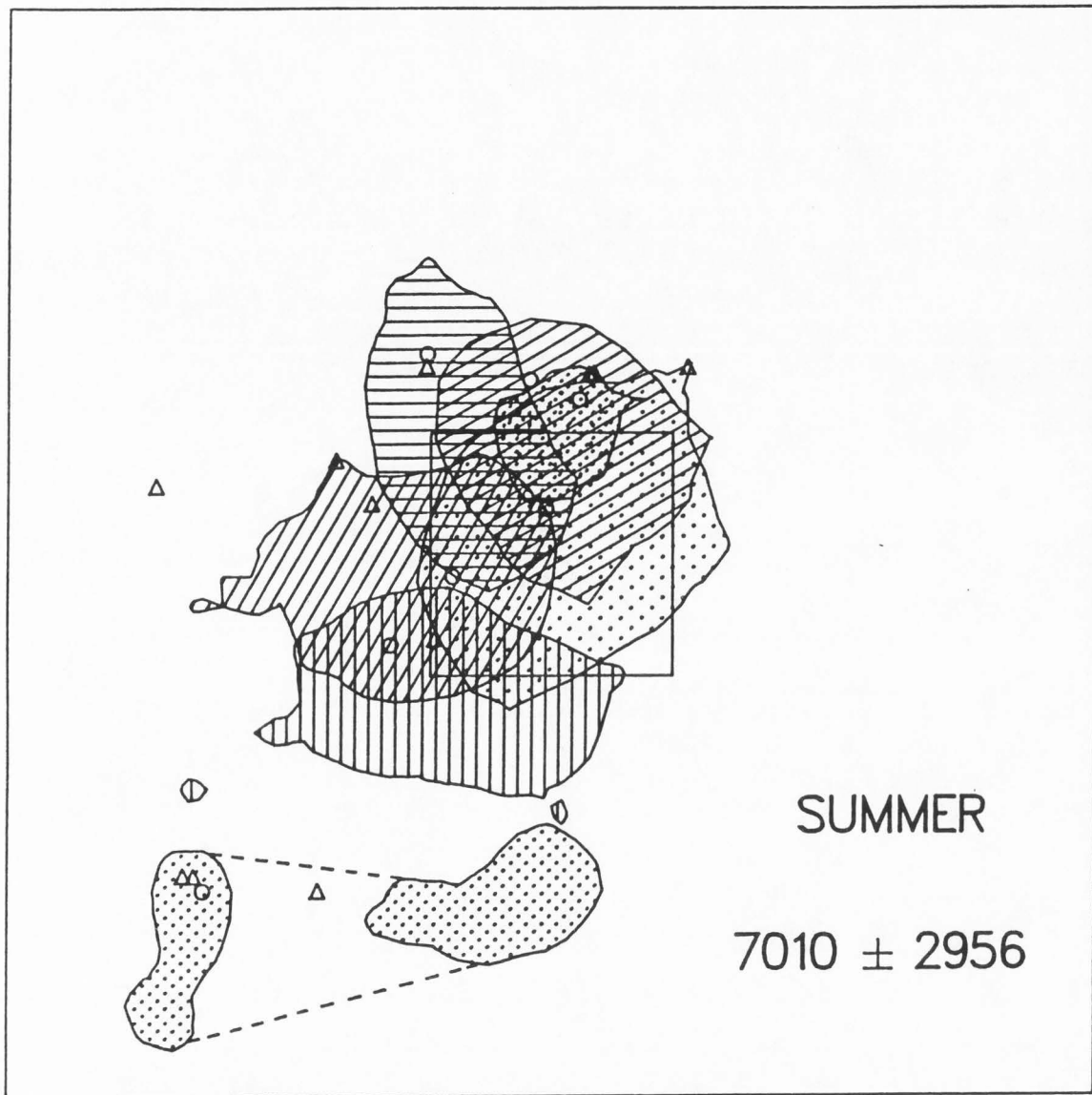
△ nest—site   ▦ female home range

○ center of activity   ▨ male home range

Fig. 26. Seventy-five percent harmonic mean home ranges of radio-tracked mice on the shrub-removal grid in summer. Mean home range size (m2) ± one standard deviation provided.

had no significant differences in home range sizes, although in summer the largest home ranges on each grid were held by males and the smallest (control and shrub-removal) by pregnant females (3318, 5200).

On the control grid (Figs. 21, 22) home range sizes did not differ significantly between summer and winter (Table 18). Seasonal shifts in home range onto the grid in winter and off the grid in summer are suggested by these figures. This grid was located on a low, sandy rise which was shallowly covered by snow in winter and became very dry in summer. In winter, foraging was confined to these higher areas but in summer radiotracked mice foraged in the nearby moister swales.

Food addition resulted in significantly smaller home ranges than on the control grid during winter but not during summer (Table 18). In winter (Fig. 23), mice were concentrated on the grid with ranges enclosing little more than nest sites and feeders between which, when active, they made repeated caching forays. In summer (Fig. 24), home ranges expanded and were similar in size to those on the control grid (Table 18). All nest sites of mice radiotracked in summer were located off the grid, with only three as close to the grid as they had been in winter. Mice still made repeated caching forays between feeders and nest sites, hence the bimodal concentrations of activity (Fig. 24).

Deermice left the shrub-removal grid after the first snow on 12 November and remained within the cover of shrubs on the edge of the grid (Fig. 25) until snow melt in late February. Winter home range sizes were similar in size to those on the control grid (Table 18). Home ranges were relocated onto the grid after snowmelt, and in summer (Fig. 26) were significantly larger than those on the control and fed

grids (Table 18). Nest sites, during both winter and summer, were located within the boundary of shrub cover and not on the cleared area of the grid, with one exception. One of the three summer nest sites of mouse 1428 was within a ground squirrel burrow on the southern edge of the grid, 10 m from the shrub edge.

Nest sites.--During daylight, mice were located in small underground holes, in abandoned ground squirrel burrows and badger dens or in nests on the ground surface (Table 19). Some mice also dug holes into piles of loose soil deposited near the road edge. Three of the four mice making long distance forays from the west side of the food-addition grid in summer (Fig. 24) had nests under rocks piled at the base of a cliff. One mouse caught on the control grid (4403) also lived under rocks on the face of the cliff (Fig. 22). One third of the nest sites on the shrub-removal grid during summer and winter were located under piles of brush placed 10 - 20 m within the shrub boundary.

Surface locations in winter consisted of well-insulated spherical nests constructed predominantly of stripped bark. Nests were placed on the soil surface, or in a depression, among the branches of low bushes which provided structural support against the snowpack. Summer surface nests were most often a simple depression, located under overhanging branches of prostrate shrubs and lined with finely chewed grass, moss or bark stripped from sagebrush.

Nest sites, particularly mouse holes dug into the soil at the base of shrubs, and winter surface nests, were much more abundant on the food-addition than on the control grids. An estimated 63 abandoned

Table 19. Nest-site locations of radiotracked mice on the three treatment grids in summer (S) and winter (W). Numbers represent the total number of day nest-locations in each site, numbers in parenthesis are female, male locations.

Grid		Mouse hole under shrub	Badger or ground squirrel den	Surface nest or depression	Brush-pile Brush-pile	Rockpile (cliff) or dirt pile (road)
				Nest-site location		
Control	S	8 (6,2)	2 (2,0)	6 (2,4)	-	4 (4,0)
	W	5 (1,4)	5 (2,3)	0	-	0
Food-addition	S	5 (4,1)	5 (5,0)	0	-	5 (2,3)
	W	11 (8,3)	4 (2,2)	2 (1,1)	-	1 (1,0)
Shrub-removal	S	4 (2,2)	2 (1,1)	0	4 (2,2)	2 (1,1)
	W	3 (0,3)	4 (3,1)	0	4 (2,2)	1 (1,0)

bark nests, and 118 mouse holes occurred on the food-addition grid in spring 1984. Three nests and 13 mouse holes occurred on the control grid (estimates from 2 m wide strip transects walked along each trap-line). None were found on the shrub-removal grid.

Radiotracked mice frequently changed their day locations. Some mice changed nest sites up to six times during a month in winter and two weeks in summer; others remained at one nest site for the entire tracking period. Several oscillated between two or three sites, spending a few days at a time at each one. The mean frequency of nest site changes, standardized to a 10 day period is presented in (Table 20). There were no significant differences between sexes (Table 21). Changes were made more frequently in summer than in winter, and on the control, shrub-removal and fed grids, respectively (Table 20). Differences between grids were significant only in summer between the food-addition and control grids (tests of pairwise differences between means, Table 21).

Nest site sharing in summer occurred only between male/female pairs, on the non-fed grids. One pair on the control grid (female 3323, male 2356) shared the same hole for five nights after which the female moved to a new site. Another a pair (female 1524, male 2358) stayed together under a brushpile by the shrub-removal grid for seven nights before they were recaptured. Long-term nest sharing was evidenced between a pair near the shrub-removal grid in winter. This pair spent two weeks in the same brush pile nest site during December before they moved to separate nests. Two weeks later, the female moved to a badger hole, was joined after two days by the male, and both were recaptured.

Table 20. Mean frequency of nest-site changes per 10 day period for radio-
telemetered mice.

Grid	Summer $\overline{X} \pm$ SD	Winter $\overline{X} \pm$ SD
Control	3.33 $\pm$ 1.52	1.59 $\pm$ 1.63
Shrub-removal	2.42 $\pm$ 1.17	0.91 $\pm$ 0.55
Food addition	1.85 $\pm$ 0.42	0.75 $\pm$ 0.55

Table 21. Analysis of variance for the frequency of nest-site changes
of radiotelemetered mice. Significance levels: ** = 0.01;
* = 0.05; (*) = 0.10.

Source of Variation	df	F-ratio	Probability	Significance level
Grid (G)	2	3.09	0.063	(*)
Control vs. Fed	1	5.95	0.022	*
Control vs. Shrub-removal	1	0.88	0.358	NS
Fed vs. Shrub-removal	1	0.53	0.473	NS
Season (S)	1	13.08	0.001	**
G × S	2	0.23	0.800	NS
Sex (A)	1	0.05	0.831	NS

After being fitted with new transmitters in February, they shared a new brush pile nest site for four days before both disappeared. Badger/ ground squirrel burrow systems were occupied by members of the same sex during the winter. An additional female used the same badger hole as the above pair on the shrub-removal grid, and two males shared a ground squirrel burrow on the control grid.

Activity patterns.--Radiotelemetry was used to define generalized categories of activity and movement. All locations were subdivided according to two categories: whether they were at the nest site or away from the nest site, and whether the mouse was active or inactive. Activity was defined as greater than one distinct radio pulse change per minute during a 5 minute period. Mice were frequently inactive at nest sites, but were seldom inactive away from nest sites (7 out of 946 locations). All inactive away-from-nest site locations were on the food-addition grid during winter, when mice remained still for longer than 5 minutes under a shrub. This category is not used for further analysis.

Distributions of the three remaining categories, pooled over grids, are plotted for winter and summer in Fig. 27. There were no significant differences between grids in the proportion of time spent at nest sites during winter (Table 22). In summer, a lower proportion of female locations were recorded at nest sites on the shrub-removal grid than on the other two grids. No obvious explanation was evident; it could be a small sample size bias (only three females were sampled compared to five on the other two grids). More time was spent at nest sites during winter (58% of all locations) than summer (12%). In
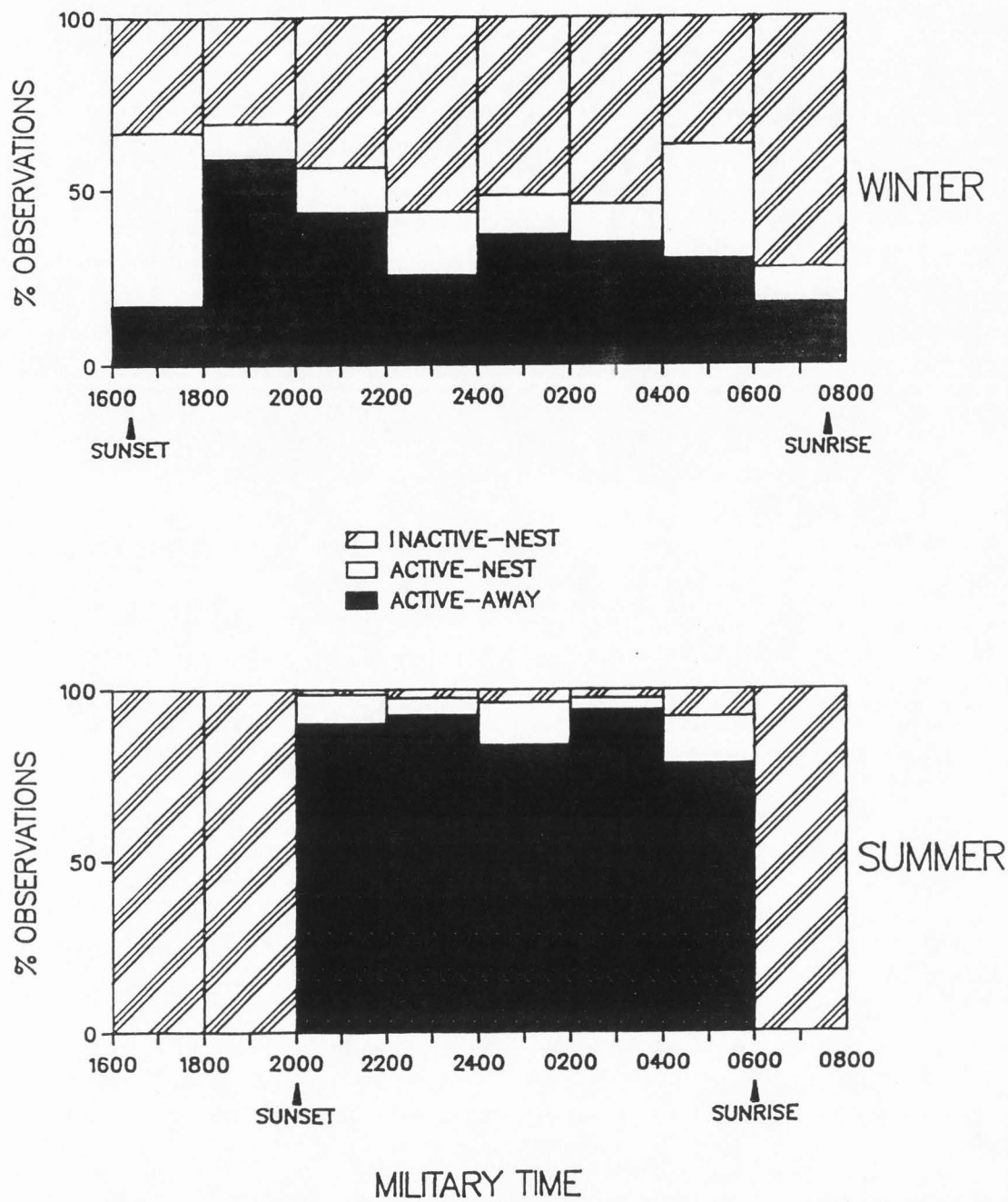
Fig. 27. Activity and location (at or away from the nest site) of radiotracked mice throughout the night in winter and summer.

Table 22. Chi-square tests for the proportion or radio locations
centered on nest sites: H = at nest site; A = away from nest site;
C = control grid; F = food addition grid; G = shrub-removal grid.
Significance levels: ** = 0.01.

Comparison:

GRIDS

		C	F	G		
WINTER	H	100	226	73	$X^2_2 = 5.15$	NS
	A	50	177	54		

		C	F	G		
SUMMER	H	45	29	13	$X^2_2 = 27.42$	**
	A	259	120	286	F vs. C $X^2_1 = 1.59$	NS
					FC vs. G $X^2_1 = 25.30$	**

SEASONS

		Summer	Winter		
	H	87	399	$X^2_2 = 354.44$	**
	A	665	281		

SEXES

		Male	Female		
WINTER	H	191	208	$X^2_1 = 0.05$	NS
	A	137	144		

		Male	Female		
SUMMER	H	15	72	$X^2_1 = 30.24$	**
	A	322	343		

winter, both sexes were inactive 73% of the time, possibly undergoing torpor (Gaertner et al. 1973, Hill 1975, Lynch et al. 1978). Females spent more time in nests during summer than males (Table 22), usually remained active (71% of nest locations), and may have been tending young or involved in caching activities. Males seldom returned to nest sites at night during summer.

Although it was not possible to determine exactly what the mice were doing in their nest sites, some of the summer activity on the food-addition grid involved seed caching. Females 2334 and 3578 made repeated caching forays between the nest sites and the feeders. Seeds were also found in the two nest sites of female 5324, 137 m from the grid edge. The female who spent the most time at nest sites on the control grid (4406) was not obviously pregnant or lactating, but had been perforated. It is possible that she may have been caching seeds in preparation for parturition. Both sexes cached seed on the food-addition grid during winter. One male died in his above-ground nest after having a transmitter implanted (he pulled the sutures out and eviscerated himself). Millet (500 g) was stored in a depression underneath the nest. Other abandoned nests, found after snowmelt in spring, also had signs of granaries associated with them. All winter-tracked mice made repeated visits between nest sites and feeders. One female (3245), for example, made 10 visits between her nest site and feeder during a 10-minute interval. Caching was not observed on the control or shrub-removal grids during winter.

Winter-tracked mice on the control and shrub-removal grids seldom left their nest sites, but remained away for long periods when they did

(up to 30 min). The general movement pattern of mice tracked for the duration of their above-ground activity consisted of rapid movement across the snow surface to a shrub which was partly visible above the snow level, submersion into the shrub, movement underneath (presumably foraging), re-emergence and travel to another shrub. Male 400, for example, spent a mean time of 11 min at each shrub visited during three complete foraging bouts.

Foraging activity in summer was concentrated at the feeders on the food-addition grid, the cleared area of the shrub-removal grid, and generally on the moister swales surrounding the control grid. The mice tracked in May on the control grid were in areas in which ant mounds were abundant. These mice freqently spent time foraging in the immediate vicinity of ant mounds.

Predation.--Those transmittered mice lost to predators or unknown causes are indicated in Table 23. In winter, predation or loss was largely confined to the non-fed grids. The one mouse lost on the food-addition grid disappeared two days after being transmittered, prior to heavy snow accumulation. Numerous weasel tracks were found in the snow near its nest area. Five of the six mice disappeared from the control grid; female 5056's transmitter was recovered from an owl pellet and male 400's from a weasel den. Male 200 was probably predated also. It was located during the day on 15 February but could not be found that night. Three of six mice disappeared from unidentified causes on the shrub-removal grid in November, and two disappeared in February.

In contrast, during summer, confirmed predation and losses due to unknown causes were confined to the food-addition grid. Two females

Table 23. The proportion of losses of transmittered mice to predation or unknown causes.

Grid	Season	
	Winter	Summer
Food-addition	1/10	5/8
Control	5/6	0/10
Shrub-removal	3/6	0/7

(5008, 3503) were eaten by weasels, and a third (5324) by a badger that
dug up its nest. Two males disappeared and may also have been eaten.
One predation attempt was detected on the shrub-removal grid. A badger
dug up the first nest site of male 1428 but the mouse escaped and moved
to a new nest site.

4.3 Trapping Bias

The home ranges obtained from radiotelemetry (Figs. 16-21) demon-
strate that the 0.71 ha trapping grids did not contain the home ranges
of the radiotracked mice in most cases. Only on the food-addition grid
in winter (Fig. 23) was this assumption approximated to any extent. On
the control grid, in summer (Fig. 22), the home ranges of all but one
mouse lay entirely outside the trapping grid. Distances moved outside
the grids during summer were large in relation to the grid sizes; the
overall mean maximum distance moved away from the grid boundaries
(Table 24) was 99.3 m. Clearly, the estimates of $\hat{N}$ cannot be equated
with the grid areas, and would be greatly biased estimators of density.
Use of the average distance moved away from the grid edge as an esti-
mate of the boundary strip width produces an effective trapping area of
7.9 ha; more than 10 times the grid size. The effective trapping area
estimated from the average maximum distance moved between traps (41.4
m) would be 2.7 ha. Home range sizes averaged 38%, 39%, and 100% of
the grid area on control, food-addition and shrub-removal grids respec-
tively. Bondrup-Nielsen (1983) indicated that if home range sizes were
greater than about 6% of the grid size $\hat{N}$ would be a biased estimator of
density, thus a correction should be made for edge effect.

Table 24. Maximum distances radiotracked mice moved away from the edge
of the trapping grids; and maximum home range diameters obtained
from trapping versus radio-tracking. Significance levels with
Students t test: ** = 0.01, * = 0.05.

Grid/Mouse #	Radiotracking maximum home range diameter (m)	t	Trapping maximum distance between traps (m)	t	Radiotracking maximum distance from grid edge (m)
Control					
F 3323	91.2		35.1		90.4
F 3318	64.0		29.7		41.6
F 4125	100.0		66.4		92.0
F 4406	81.6		-		64.8
F 4402	100.0		49.5		27.2
F 4403†	-		-		220.8†
M 2356	128.0		50.5		107.2
M 4202	80.0		40.8		72.0
M 4401	253.0		35.7		224.0
$\bar{X} \pm S$	112.2 ± 59.9	2.95*	44.0 ± 12.5	2.20*	104.4 ± 71.4
Food addition					
F 3503	202.4		22.1		156.0
F 5008	28.0		15.7		10.4
F 2334	134.4		42.6		104.8
F 5324	180.8		15.7		137.6
F 3578	109.6		19.8		93.6
M 4036	264.0		39.6		202.4
M 4025	203.2		47.0		125.6
$\bar{X} \pm S$	160.3 ± 77.0	4.45**	28.9 ± 13.6	3.88**	118.6 ± 59.7
Shrub-removal					
F 1524	152.0		81.9		34.4
F 5200	68.0		25.2		22.4
F 3556	168.0		15.7		157.6
M 1428	180.0		75.4		114.4
M 5157	148.0		44.3		68.0
M 2358	114.4		70.0		33.6
M 5201	156.8		40.8		93.6
$\bar{X} \pm S$	141.0 ± 38.1	5.21**	50.5 ± 25.7	1.15NS	74.9 ± 49.8

† distance from nest-site to edge of grid

Use of the mean maximum distance moved between traps on each grid (MMDM) to estimate the widths of boundary strips would still provide biased density estimates in this study. Between trap movements on the control and food-addition grids were of a much smaller scale than were the actual distances, measured by radiotelemetry, that mice moved from outside the grid to the grid edge (Table 24). I initially used the method of Wilson and Anderson (1985b) to estimate density, but abandoned the attempt due to obvious bias. Density estimates would be too high because the maximum home range diameters were underestimated by the trapping MMDM (Table 24). An adjustment factor could not be introduced because there was little correlation between radiotracking and trapping distances. Within grid correlations produced coefficients of $r = -.19$, $r = .51$, $r = .26$, ($n = 7$) on control, food addition and shrub-removal grids respectively. There was no correlation between distances pooled across grids ($r = .01$, $P=.01$, $n=21$). Inter-grid comparisons would also be distorted, e.g., the food addition grid had the largest radiotracking home range diameters but the smallest MMDM between traps.

Edge effect is thought to be detectable in trapping data as a greater proportion of captures in the outer perimeter of traps (Tanaka 1972, Schroder 1981, Bondrup-Nielsen 1983). Using this criterion, edge effect was not apparent in this study despite the extreme edge effect illustrated. For example, on the control grid in summer (Fig. 22), the home ranges of 7 of the 8 radiotracked mice were outside the trapping grid. All of these individuals were trapped inside the perimeter traps, with no detectable edge effect from trapping data (mean number

of captures per mouse = 4.25, range 1-8).

Use of $\hat{N}$ as an index to density assumes that the edge effect is similar for all treatments. If animals were attracted to traps from different distances outside the grids, then the differences in $\hat{N}$ between treatments (Fig. 10) might simply reflect differential edge effect. The distances radiotracked mice moved outside the food-addition grid were large, but they were not significantly larger than those outside the control or shrub-removal grids (Table 25); the presence of baited traps appeared sufficient to induce movements onto the control grid. Thus, assuming that the distances radiotracked mice moved away from the grid edges are representative of the population as a whole, the differences in $\hat{N}$ are probably indicative of density changes in the vicinities of trapping grids. The estimated $\hat{N}$'s can at least be regarded as comparable indices of population size responses to the treatments. Although some bias may be present, significant differences between other population parameters (e.g., breeding, sex ratio, fidelity) on the three treatment grids reinforce the conclusion that differences in population size were not simply a function of trapping bias. The observed temporal fluctuations in $\hat{N}$ which occurred, irrespective of treatment (e.g., fall increases), may be partly attributable to trapping bias.

Table 25.   Analysis of variance for the maximum distance radiotracked
mice moved away from the edge of the trapping grids.

Source of variation	df	M.S.	F-ratio	Probability	
Grids	2	3515	0.91	0.58	NS
Error	20	3849			
Total	22				

Individual 95% confidence intervals for mean based on pooled
standard deviation (62.04)
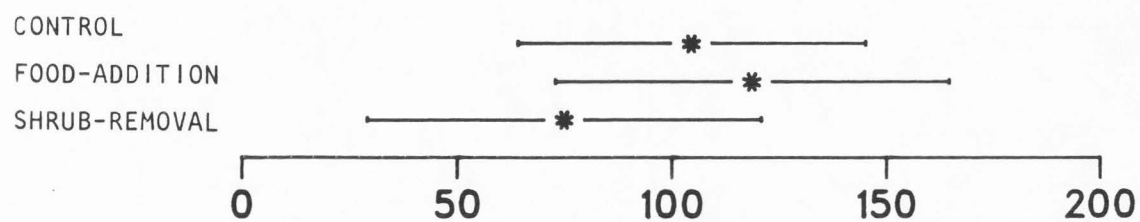
CHAPTER V

INFLUENCES OF FOOD AND SHRUBS ON DEERMICE: DISCUSSION

5.1 Trapping Bias

An important result of this study is the illustration of the large home range sizes of radiotracked mice in relation to the size of the trapping grids; consequently the large edge effect. This result has implications not only for the estimation of density but for other commonly used population parameters. I have largely avoided using terms such as survival, dispersal, immigration or emigration, because of the high bias likely to result in estimates of these parameters from the trapping data. For example, mice may live near the grids but only be attracted to them when food supplies are scarce. New captures would therefore not necessarily be recruits or immigrants (i.e., "dispersers", Sullivan 1980, Van Horne 1981). They could simply have undergone home range shifts within the local area. Dispersal is equatable with immigration or emigration only if individuals leave their home areas (Lidicker 1975). By the same criteria, disappearance from the grid is not necessarily equatable with emigration or death; nor is fidelity equivalent to survival. Such associations are, however, commonly made in studies of deermice (e.g., Flowerdew 1972, Fairbairn 1977, 1978a, Taitt 1981, Wolff 1985a). Grid sizes in these studies were similar to mine (0.8-1.0 ha).

The assumption that between-trap movements are indicative of the extent of movements outside the grids was shown to be incorrect. Many

trapping studies indicate that home range size is inversely related to density or population size (e.g., Stickel 1960, Sheppe 1966, Parmenter and MacMahon 1983) and to resource availability (Miller and Getz 1977, Bowers and Smith 1979, Taitt 1981). Other investigators found no such relationship (Metzgar 1971, Van Horne 1981, Wolff 1985b). Radio-tracking in this study showed that home range size was not directly related to density or to food availability on the trapping grids, but rather to the dispersion of food and cover in the local area. By contrast, MMDM's between traps decreased in response to food addition. Consequently, home range sizes estimated from trap locations would decrease and would be inversely related to density and food levels on the grids. These results suggest why relationships determined from trapping data are inconsistent. Trapping studies also show that male deermice have larger home ranges than do females (e.g., Williams 1955, Myton 1974, Metzgar 1971, 1979, Mihok 1979, Taitt 1981, Van Horne 1981, Wolff 1985b). In this study males sometimes moved greater distances between traps, but the telemetry results indicated no sexual differ-ences in home range size. Other radiotracking studies show similar results (Mineau and Madison 1977, Madison 1977). Again, trapping bias may be involved, although I recognize that small sample size may lead to type 2 error in the radiotelemetry comparisons.

Mice were attracted to the food-addition and shrub-removal grids by trapping and the experimental treatments. Radiotracking on the control grid indicated that mice whose home ranges lay entirely outside the grid were being attracted solely by the baited traps. That traps attracted deermice was also seen on the shrub-removal grid. Two radio-

tracked mice systematically searched each trap along the traplines on this grid one night after traps were closed. These results imply that use of capture locations to indicate microhabitat preferences may be meaningless, if baited traps draw animals from their usual foraging locations.

An additional implication of the large distances mice were attracted to the grids is that any treatment applied to the grids cannot be regarded as homogeneous. That is, many mice trapped on the grids experience conditions other than those imposed on the grid area. Large edge effect may also invalidate independence of replicate grids, if the grids are too closely spaced.

5.2 Food Resources as a Limiting Factor

The numerical response to food supplementation implied that deermice were food limited. However, sex ratios indicated that females responded to a greater extent in spring and males responded more in fall. Similar results have been obtained in other studies (Gilbert and Krebs 1981, Taitt 1981, Wolff 1985b). Increased population sizes on "fed" grids have been attributed to decreased home range sizes (estimated from trap locations or shorter inter-trap movements), hence greater packing of animals onto the grids (Taitt 1981, Gilbert and Krebs 1981). In this study, radio tracking indicated that food did not reduce home range sizes in spring and summer. Metzgar (1973) and Wolff (1985b) similarly concluded that food did not affect home range size. Home range shape did change and the part that was on the grid was smaller than the ranges on grids where food was absent. Considerable

home range overlap on the food-addition grid probably contributed to the increased population size during summer. Higher densities during winter could be attributed to decreased home range sizes.

Food enhanced female reproductive rates in spring and fall on the supplemental grids. At these times natural food supplies are scarce. Maximum seed production occurs between late June and early August (personal observation, Kelrick 1988). Invertebrates are scarce in early spring, reaching a small peak in numbers in June and maximum numbers in late August and September (Parmenter, unpublished data). Lactating females require up to 200% of their non-breeding energy requirements, most of which is obtained through increased food intake rather than from fat accumulations (Millar 1975, Stebbins 1977, Millar 1979, Millar and Innes 1983). This energy was not available in early spring or late fall on control grids. Increased reproductive rates were reflected in greater recruitment of juveniles in spring 1984 (as found, for example, by Hansen and Batzli 1978, Taitt 1981) but not during spring 1982. This is probably a reflection of earlier trapping in 1984 when the differences in breeding status of adults on fed and non-fed grids were more extreme.

It has been suggested that the length of the breeding season for deermice in temperate winter climates is entirely determined by food availability (Sadleir et al. 1973). Taitt (1981) confirmed this in southern British Columbia, where deermice bred in winter when food was supplied. In my study area, breeding ceased between November and February despite availability of food. This might have been due to the direct influence of freezing temperatures (Millar and Gyug 1981) or the

combined effects of decreasing photoperiod and cold temperature-induced reproductive regression (Lynch et al. 1980, Glass and Lynch 1981, Lynch and Wichman 1981). The physical effects of temperature and snow cover on restricting the movements and activity of mice, and inducing changes in their sociality (e.g., social nesting for thermal benefits, Lynch et al. 1978, Vogt and Lynch 1982, Andrews and Belknap 1986), may also induce reproductive regression during winter.

If food availability is a prominent limiting factor on the population, then grid fidelity should be enhanced by higher levels of food resources. This was true for adult and subadult females in the spring when breeding intensity was high. Male fidelity was higher on fed grids only in fall after breeding had virtually ceased. Juvenile fidelity was also greater in fall despite higher recruitment in summer. These results and the observation that following high prebreeding densities in the spring of 1984 neither female nor male fidelity was improved by feeding suggests that food is only proximately limiting for both sexes.

The extent of the sex ratio skew in spring reflects differential distribution of sexes according to resource levels. Adult females predominated in food-rich habitats (fed grids), and males were more abundant in relatively food-poor habitats (control grids). Sex ratios were equal on the shrub-removal grid, where food levels were probably intermediate (Section 5.3). Skewed sex ratios in other studies may also be attributable to differences in food levels. Similarly, Fordham (1971) and Taitt (1981) trapped a higher proportion of females on food supplemental compared to control grids (even versus male biased

ratios). Bowers and Smith (1979) found more females in moist compared to xeric microhabitats; and less clearly, Sullivan (1979) and Van Horne (1981) thought females were more abundant on logged compared to unlogged coastal forests. These results strongly support the predictions of Sadleir (1974), Fairbairn (1977) and Van Horne (1981): if adult female distribution and survivorship is primarily governed by food availability in the early breeding season then breeding and survival of females will be greater in food-rich habitats and one might expect a male sex ratio skew in food-poor habitats. The aggression associated with the extreme skew in spring 1984 suggests that differential sex distributions are actively maintained.

In contrast to those of adults, subadult and juvenile sex ratios were skewed towards males on fed grids in the spring and summer. It is possible that the initial captures of juveniles could be male biased due to disparate ratios at birth (Smith 1967, Terman and Sassaman 1967, Canham 1970), faster growth rates (as found for Microtus, Myers and Krebs 1971) and better survival than females as nestlings (Hansen and Batzli 1978). Juvenile males may also be attracted to the trapping grids upon weaning. Long distance movements of P. leucopus occurred before they reached 12 g (Hansen and Batzli 1978), and young males had shorter periods of residence and greater turnover rates (on 1 ha trapping grids) than females (Wolff and Lundy 1985). Many trapping studies, including this one, show that between-trap movements are often greater for males. If this is a reflection of greater home range sizes, then commonly observed male biased sex ratios (Fairbairn 1978a, Taitt 1981, Van Horne 1981, this study) could arise because males are

drawn to traps from a greater distance from outside the trapping grid than are females. If food was an attraction, one might expect an even greater male biased sex ratio on fed grids. My radiotracking results belie differential movement between sexes or treatments for adults. Therefore it is my belief that the differential adult sex ratio skew on fed and non-fed grids is not due to trapping bias, and is primarily a result of social interactions mediated by differences in resource levels. I suspect that the male skew on fed grids of both subadults and juveniles may be a reflection of trapping bias and greater mobility of young males.

In summary, my results demonstrate that food is a limiting factor on the deermouse population, especially in winter when greater numbers of both sexes on food-rich areas could be attributed to decreased home range sizes. During the breeding season, numbers of both sexes, but particularly males, declined despite the presence of food. Temporal variability in grid fidelity of juveniles and adults/subadults, and in sex ratio skew appears to be related to the breeding status of the adult population. As evidenced by their lower breeding response, lower spring fidelity and sharper decline in numbers, males appear to be less strongly food limited than are females during the breeding season. These results suggest that food availability is only proximately limiting. Social factors, mediated by differences in resource levels, may ultimately determine breeding season densities.

5.3 Shrub Cover as a Limiting Factor

Parmenter and MacMahon (1983) found no differences in deermouse population sizes, home range sizes, spatial distributions of captures, sex ratios or age structure when they compared the shrub-removal grid with a control grid in 1980/81. Their comparison was based on trapping between the months of May and September. Similarly, I found no significant differences in estimated population size in June, September and October in age structure or distances moved between traps. Sex ratios were similar in fall but were significantly different in spring. The radiotelemetry results illustrate that the estimated $\hat{N}$'s represent mice which used, but were not restricted to the area cleared of shrubs. Because mice used both cleared and shrubby habitats this treatment represents the effects of large clearings, rather than the absence of shrubs, on population parameters. Shrubs, and the piles of brush cleared from the grid, were used as nesting sites during my study. It is likely this was also the case in 1980/81. Therefore the conclusion that shrubs were unimportant to deermice (Parmenter and MacMahon 1983) probably pertains only to foraging habitat. Trapping, radiotracking and snowtracking indicated that deermice vacated the area cleared of shrubs during the period of winter snow cover. At this time mice used shrubs as a shaft to access ground and snow surfaces. Foraging was carried out beneath shrubs, which probably provided a subnivean snow-free space, but travel occurred on the snow surface. Shrubs were maintained as nesting sites in winter, and in some situations (e.g., on food-addition grids) provided structural support against the snowpack for nests built on the ground.

Differential sex ratios (between shrub-removal and control grids in the spring of 1984, but not during 1980/81) coincided with differences in the quality of foraging habitat. Soil seed reserves, and grass and forb cover were not affected by shrub removal in 1980/81 (Parmenter and MacMahon 1983); although grass cover was beginning to increase by August 1981 (Table 1). By September 1983, shrub removal had promoted an increased grass and forb cover, which was also higher than the cover on my food-addition and control grids (Table 1). Soil seed reserves were not analyzed in 1983, but increased grass/forb cover probably resulted in increased production of seeds. Arthropods may also have increased with the increasing grass/forb cover (Waterhouse 1955, Larmuth 1979). These changes promoted favorable foraging habitat for deermice during the snow-free season, as indicated by the movements of radiotracked mice, the high overwinter grid fidelity, and the higher proportion of females using the grid in spring compared to the control grids. The presence of more mice on this area in March 1984, than on the control grids, may have been attributable to higher overall food levels, and the release upon snowmelt of seeds which were not available during winter. The decline in June may have been a function of social interactions rather than a decline in preference for the area.

Some foraging decisions represent a trade-off between predation risk and resource availability (e.g., Pulliam 1975, Caraco et al. 1980, Krebs 1980, Grubb and Greenwald 1982, Schneider 1984). Deermice in deserts may restrict their foraging activity to shrubs because of high predation risk in open areas (Thompson 1982b, Kotler 1984, 1985). This hypothesis presupposes that predation risk is greater in open areas

than it is under shrubs; the major risk being owl predation (Clarke 1983, Kotler 1985). Alternatively, selection of shrubs as foraging habitat in deserts may be a reflection of heterogenous seed distribution patterns. Seeds tend to accumulate in the soil and litter under shrub canopies (Nelson and Chew 1977, Thompson 1982b, Mojave desert; Parmenter and MacMahon 1983, Kelrick 1988, this study area).

Peromyscus maniculatus is an opportunist. It is frequently the first species to colonize recently disturbed areas (e.g., Parmenter and MacMahon 1983 and citations therein, Hingtgen and Clarke 1984) and is behaviorally plastic (Wywialowski 1987). It appears to be restricted in its habitat use by species with greater habitat specialization (Hallet et al. 1983). Experimental studies show that P. maniculatus may be competitively displaced by other species (Crowell and Pimm 1976, Abramsky et al. 1979, Holbrook 1979, Munger and Brown 1981, Brown and Munger 1985). In this study P. maniculatus was the predominant species in the rodent community, thus interspecific displacement was probably not a major consideration in its habitat choice. Predation risk during summer did not appear to be greater in the open than under shrubs. Incidences of predation during summer on the shrub-removal and control areas were low and mice showed no avoidance of open areas that were rich in food. Much of the foraging time was spent either on the shrub removal area, or around ant mounds and in smaller grass patches. Deer-mice tended to stay under cover, where possible, when food resources were freely available. Where feeders were placed in interspaces on the food addition grid, it was noted that piles of seed husks occurred under the nearest shrub, rather than close to the feeder. Such

behavior might decrease vulnerability to avian predators. The most
abundant predators in this study appeared to be short tail weasels
(Mustela erminea) although owls, badgers, coyotes and bobcats were
present. Weasels are small, so shrubs might provide mice with less
protection from weasel predation than, for example, from owls (Kotler
1985). Wywialowski (1987) confirmed experimentally that deermice
showed only a small inherent preference for areas with greater cover
density, in comparison to a microtine habitat specialist. Furthermore,
differences in cover density did not affect its vulnerability to preda-
tion by a mustelid. Differences in habitat specific predation risk,
combined with higher shrub densities or greater ground cover in inter-
spaces, may explain the contrast with Kotler's (1984) results in the
Great Basin Desert. The choice of foraging habitat by deermice on this
study area appears to be a function of opportunistic exploitation of
food resource distributions rather than predation risk. Risk from
avian predators might contribute to foraging under shrubs within
shrubby habitats, but shrubs are probably favorable foraging sites due
to greater seed accumultion at their bases than in interspaces
(Parmenter and MacMahon 1983, Kelrick 1988).

Predation by owls may have been more important during winter, when
mice could easily be seen on the snow surface. This is suggested by
the high level of winter predation on the control grid, where mice
moved longer distances and were predated more than they were on the
food-addition grid. One transmitter was found in an owl pellet at this
time. Owls were commonly heard during winter but not summer. Vulner-
ability to predation appeared more closely related to population

density than to cover density during summer. Heavy predation on the high density food-addition grid may relate to a numerical response by predators to the increased prey density. Although the grids were too small to evaluate predator densities, captures of weasels occurred only on fed grids. The predictable movement patterns of foraging mice, between feeders and nest sites, might have exacerbated their vulnerablity to predators.

In summary, the absence of shrubs increased grass and forb cover during summer and provided attractive foraging habitat. Changes in demographic structure resulted, intermediate between those on the control grid and the changes produced by food-addition. This response appeared to arise from increased habitat heterogeneity; shrub clearing promoted increased food levels on the grid but mice still required shrubs for nesting cover.

5.4 Intraspecific Sociality and the Spring Decline

A spring decline in population size occurred on all grids, but most dramatically on the food-addition and shrub-removal grids in the spring of 1984. Declines were most severe where food was abundant, where early spring population sizes were high (e.g., March 1984) and where snow melted early. The level of agonistic behavior, in combination with winter to summer home range expansions on the food-addition and shrub-removal grids, and the absence of wounding following the decline in August 1984, suggest that much of the decline is socially induced. Reproductive aggression was most severe in food-rich areas. Following snowmelt in spring, the shrub-removal grid was

repopulated at fall levels. The decline between March and May/June could be attributed, at least for males, to reestablishment of territories by residents of the previous fall.

The predominantly female response to food-addition, female skewed sex ratios and low fidelity of juveniles and males in spring and summer on food-rich areas are consistent with the following hypothesis: social interactions are a regulating mechanism during the breeding season, and those interactions are driven by inter-female defense of high quality breeding habitat (Metzgar 1971, 1980, Hansen and Batzli 1978, Taitt 1981, Taitt and Krebs 1983). The greater degree of male wounding, particularly of breeding, heavy weight, resident males, combined with the lesser degree of wounding of females, additionally of those which were of lighter weight and non-breeding, lends credence to the following suggestion: on high density habitats males, whose home ranges overlap, compete aggressively among themselves for access to females; dominant females have more mutually exclusive area-association and defend breeding habitat (Wolff 1985b). Adult males were heaviest on fed grids in March 1984, when food enhanced breeding and aggression was intense. Heavier males are more aggressive (Sadleir 1965, Fairbairn 1977) and are probably dominants (Iverson and Turner 1974). Continued interaction between dominant males who were not tightly area-associated would lead to a high level of inter-male wounding, particularly where female density was high (Terman 1984). In contrast, area-specific association, with perhaps territorial defense of nest sites and tolerance or avoidance of known neighbors at home range boundaries (Wolff et al. 1983, Wolff 1985c) would lead to little wounding among breeding

females. Breeding adult females are aggressive (Wolff 1985c) and might exclude lighter weight, non-breeding females, inflicting some injury upon them. Aggression from both sexes would lead to exclusion of juveniles (Sadleir 1965, Healey 1967, Halpin 1981, Metzgar 1971, Van Horne 1982) or subordinates (Spencer and Cameron 1983) from more favorable habitats.

The intensity of the spring decline and spring female sex ratio skew coincided with high population density in high quality habitat. Together with the levels of wounding on the three radiotelemetry grids, this implies density dependant social interactions. However, temporal, as well as spatial variability in habitat quality may induce variations in social structure within an area that are not directly related to estimates of crude density (Van Horne 1981). Social strife, as indicated by the wounding levels on all grids, was density dependent on a broad scale in that it occurred only following high fall densities in 1983 but not following lower fall densities in 1981 or 1982. Wounding on a local scale appeared to be related to the limited availability of patchy breeding habitat in a temporally and spatially heterogenous environment, independant of density. Wounding was not only an artifact of artificially high densities on the food-addition grids but occurred at a similar intensity on control grid 1 where snow melted early compared to the surrounding area. The dispersion of home ranges corroborates the suggestions of Metzgar (1971) and Wolff (1985a, 1985d) that at low densities habitat is non-saturated by home ranges and aggression is lacking, while at high densities overlap is increased and aggression is high. The observation of paired nest sharing on the non-fed grids

and absence nest sharing on the food-addition grid supports the notion that monogamy may be prevalent at low densities and polygyny at high densities (Metzgar 1979). Lack of habitat saturation and unvariant home range sizes at low densities appear to preclude sudden spring declines.

Female resource defense does not appear to be predominantly a function of food, home ranges expanded despite feeding. Locations of suitable nest sites may be partly responsible for the spring home range expansions and population decline on the food-addition grids. Although sufficient numbers of mouse holes were counted on grid 8 to house individually the maximum number of mice caught at any time, these may have been unsuitable for breeding and too closely spaced to prevent breeding interference (Wolff and Lundy 1985, Wolff 1985c). Predation pressure possibly contributed to the choice and density of nest sites. All nest sites of summer-tracked mice on grid 8 were subterranean or within rock piles and were away from the grid. Adherence to those nests was greater than on the control grid (grid 7) where, in addition to similar sites, surface nests were used frequently. Mammalian predators would be more likely to extract a mouse from a surface nest and may concentrate their searches on such nests at high density. Predation of radiotracked mice was high on the food-addition grid in spring and summer, and was probably directly responsible for part of the spring decline on the high density grids. Those mice excluded from these grids may have moved to poorer breeding habitats (Metzgar 1971, Van Horne 1982), but the fate of many during spring 1984 was socially induced mortality as a result of heavy wounding, rather than dispersal.

The gradual spring decline on the control grids, and part of the decline on the other grids, may involve a number of factors, none of which can be clearly isolated from this study. The decline may include a continuation of winter mortality. The redistribution of home ranges in spring (e.g., on grid 7 from the dry ridges in winter to the moister swales in summer) combined with decreased intrasexual home range overlap (indicated by the radiotracked home ranges on grid 7) was probably a major contributor. Lack of habitat saturation (as on grid 7, or following the ephemeral concentration on grid 1) would obviate the need for overt aggression. Part of the decline may also be due to increasing food availability in the local area, diet expansion (Taitt 1981) and subsequently less attraction to baited traps. Despite the probability of some trapping bias, the dramatic spring declines on the food-addition grids, and their associated manifestations, indicate that much of the decline in food-rich habitats was due to social interactions, home range expansion and predation.

5.5 Population Fluctuations and Regulating Mechanisms

Habitat heterogeneity can lead to uneven distributions of small mammal sex and age classes (VanHorne 1982, Spencer and Cameron 1983, Kincaid and Cameron 1985). This study indicates that socially induced variation in population density and demographic structure was a localized phenomenon. Spatial variation was induced in response to habitat manipulations of food availability and shrub cover, and also occurred temporally as a result of patchiness in snow cover. Such small-scale

variations have implications not only for the social consequences of animal movements e.g., socially subordinate animals may be relegated to adjacent less optimal habitats, or "dispersal sinks" (Lidicker 1975, Gaines and McClenaghan 1980, Van Horne 1981, Stenseth 1983), but also for population fluctuations. Annual fluctuations in population density and the inconsistencies regarding such fluctuations in the literature, may result from localized movements into and out of habitat patches of different quality, according to the physiological status (breeding condition) of the population and the dominance status of the individual. Changes in susceptibility to traps may enhance such fluctuations. For example, fall increases in deermouse population size (on grid sizes of 0.8-1.0 ha) are often obtained (e.g., Sadleir 1965, Petticrew and Sadleir 1974, Fairbairn 1978a, Gilbert and Krebs 1981, Taitt 1981, Van Horne 1981, Millar and Innis 1983). In absolute numbers caught the largest fall increases are between 12 to 25 individuals in populations ranging from 10 to 40 per ha. Most studies enumerate the number of animals caught, or the minimum number alive (Krebs 1966) and have little, if any, replication. With no estimate of standard error it seems potentially fallacious to unequivocally attribute these increases to increased survival and recruitment (e.g., Sullivan 1979, 1980, Van Horne 1981) or to dispersal (Fairbairn 1978a). I suggest that even statistically validated fall increases (e.g., those which occurred on both the food-addition and control grids in October 1982, Fig. 10) may simply be a function of increased attraction to traps as a result of decreasing local food availability, and greater fall mobility due to

reduced territorial behavior. It is likely these increases are facili-
tated by decreased aggressiveness of the adult population (Sadleir
1965, Healey 1967, Fordham 1971, Petticrew and Sadleir 1974, Fairbairn
1977). Dispersal, survival and recruitment may not be necessary to
account for movements and population fluctuations when the scale of
habitat variation is small in relation to the distances moved by deer-
mice.

Yearly differences were evident in both fall and early spring
population sizes. The higher fall numbers in 1983 compared to the
previous two years, appeared to be a generalized phenomenon in the
western U.S. (Johnson 1986) and may relate to the unusually wet summer
(372 mm above average recorded at the Kemmerer NOAA station). The
higher early spring (March) population sizes on food-addition grids in
1984 compared to 1982 were probably related to the combination of high
fall population sizes and the early and continuous, deep snowcover
(Fig. 1) which allowed the construction of surface nests on the grid.
The 1984 spring melt period was rapid, and lacked the freeze/thaw,
snow/melt cycles experienced in March 1982, which can lead to energy-
stress and mortality in small mammals (Sauer 1985, Pruitt 1984).

Despite the higher fall population sizes in 1983, spring popula-
tion sizes did not differ significantly between the three years on
control grids, and by June 1984 the population sizes on food-addition
grids had declined to the 1982 levels. There thus appears to be densi-
ty dependent regulation of numbers towards a steady early summer popu-
lation size, which is influenced but not determined by food levels, and
may depend on a minimum home range size required for breeding (Wolff

1985b). On food-addition grids the regulating factors included spring home range expansion, socially induced spring mortality and predation; with perhaps some dispersal. The extent of overwinter mortality may depend on interactions between depth of snow cover, food availability and predation. Where food was abundant (food-addition grids) the advantages of heavy snow cover (insulation, e.g., Pruitt 1984, nesting cover and reduced predation risk) were realized as low winter mortality. Heavy snow cover may not be an advantage on low food quality areas, because of restricted foraging habitat (as seen on the shrub-removal grid). Predation risk was increased when deermice crossed the snow surface between patches of foraging habitat. The regulating factors on these areas included winter predation, and redistribution of home ranges in spring.

5.6 Summary

1. Deermouse populations in this ecosystem did not appear to be influenced by competition from harvester ants during the period of this study. Some facilitation by ants may occur, but the area cleared of shrubs may not have been sufficiently large to produce a response detectable by trapping.

2. Food was limiting for deermice only to the point that social interactions during the breeding season placed a limit on maximum densities. Food reduced home range size in winter but not during the breeding season.

3. The absence of shrubs prevented winter use of the shrub-cleared area, but during summer provided attractive foraging habitat.

Enhanced food levels, from increased density of grasses and forbs, promoted changes in demographic structure that were intermediate between the control situation and that on the high density food-addition grids. Deermice still used shrubs around the edge for nesting cover and for additional foraging habitat.

4. Both food addition and shrub removal enhanced the quality of breeding habitat and promoted conditions which led to a socially induced spring decline.

5. The intensity of the spring decline and associated aggressive behavior was density dependent, but also related to the limited availability of patchy resources in a spatially or temporally heterogenous environment.

6. Spring declines followed high fall densities and were initiated by home range expansions and agonistic interactions at the onset of breeding in high quality habitats.

7. Aggressive behavior may lead directly to spring declines through intrasexual exclusion of subordinates by both sexes. Individuals excluded from these areas may shift their ranges to poorer adjacent habitats, but indications were that during the 1984 spring decline on food-rich habitats the fate of many of these subordinates was socially induced wounding mortality.

8. Although the evidence is circumstantial, predation appears to contribute to the spring decline in high quality habitats both directly, and by increasing the dispersion of residents to safe nest sites.

9. Trapping bias, as well as local habitat heterogeneity, may be responsible for much of the variability in home range sizes, population

fluctuations and inferences made about social systems in previous studies.

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APPENDIX

Table A1. The number of mice caught on combined fed, and combined non-fed grids subdivided by sex and age.

Weight (g)	Grid	Sex	Sept 81	Mar 82	Jun 82	Aug 82	Oct 82	Apr 83	Sept 83	Oct 83	Feb* 84	Mar 84	May* 84	June 84	Aug+ 84
≤13	Fed	F	34	0	19	3	14	2	17	3	0	7	4	7	6
		M	29	0	32	15	7	0	14	2	0	2	10	13	4
		TOTAL	63	0	51	18	21	2	31	5	0	9	14	20	10
	Non-fed	F	46	1	12	7	13	1	31	4	0	0	0	4	0
		M	38	0	12	12	7	3	25	0	0	0	1	0	1
		TOTAL	84	1	24	19	21	4	56	4	1	1	1	4	1
14-16	Fed	F	43	8	10	21	42	10	57	54	23	3	3	9	3
		M	61	8	23	37	51	4	46	29	3	1	4	9	7
		TOTAL	104	16	33	58	93	14	103	83	26	4	7	18	10
	Non-fed	F	44	17	4	14	37	9	99	27	6	1	0	1	1
		M	66	11	13	28	51	4	94	14	1	0	0	9	5
		TOTAL	110	28	17	42	88	13	193	41	7	1	0	10	6
≥17	Fed	F	12	139	93	43	42	58	32	64	49	140	120	47	7
		M	22	100	62	48	51	81	58	87	82	88	33	21	4
		TOTAL	34	239	155	91	156	139	90	151	131	228	153	68	11
	Non-fed	F	29	43	25	26	38	62	66	24	11	27	15	11	5
		M	32	70	33	34	57	78	77	44	38	35	23	13	2
		TOTAL	61	113	58	60	95	140	143	68	49	62	38	24	7
≤13 g	Shrub-removal	F							3	0	0	0	0	1	
		M							5	1	0	0	1	2	
		TOTAL							8	1	0	0	1	3	
14-16		F							20	16	2	8	0	0	
		M							16	10	0	1	0	1	
		TOTAL							36	26	2	9	0	1	
≥17		F							9	15	2	24	29	11	
		M							13	19	5	28	28	7	
		TOTAL							22	34	7	52	57	18	

* trapped 2 nights only
+ grids 7 and 8 only

Table A2. Results of logit model tests (z values) on sex ratios of
adults and subadults; tests for differences between treatments by
date. Significance levels: ** = 0.01; * = 0.05, (*) = 0.10.

September 1981-September 1983	1 9 8 1		1 9 8 2			1 9 8 3	
	Sept.	Mar.	Jun.	Aug.	Oct.	Apr.	Sept.
Fed vs. Non-fed	0.508	-2.796**	-2.344*	-0.590	0.510	0.344	0.663

Sept. 1983-June 1984	1 9 8 3		1 9 8 4			
	Sept.	Oct.	Feb.	Mar.	May	June
Fed vs. Non-fed (1,7 vs. 2,8)	1.260	-0.334	-1.773(*)	-2.278*	-3.807**	-2.559*
Fed vs. Shrub-removal (2,8 vs. G)	1.061	-0.081	-0.816	-2.143*	-4.087**	-1.767(*)
Non-fed vs. Shrub-removal (1,7 vs. G)	-1.088	0.455	1.665†	1.740†	2.723**	2.360*

Grid 2 vs. G8: NS all dates, $P < 0.10$

Grid 1 vs. G7: NS all dates, $P < 0.10$

Sept. 1981-Sept. 1983: x^2 between grids within treatments all NS $P < 0.05$

Simplest Models which fit data: (Saturated = G,D,GD)

Date	Parameters omitted from model	L.R. Chi square	P-level
Sept. 1981-Sept. 1983	GD	13.68	0.033*
	None	0.00	1.000
Sept. 1983-June 1984	GD	41.56	0.003**
	None	0.00	1.000

Table A3. Results of logit model tests (z values) on the percentage
of adults in breeding condition; tests between treatments/grids and
sexes by date. Significance levels: ** = 0.01; * = 0.05, (*) =
0.10.

Sept. 1981-Sept. 1983		Mar.	June	Aug.	Oct.	Apr.	Sept.
Fed vs. Non-fed	Female	-0.287	2.555*	0.278	1.687(*)	0.747	-1.570
	Male	0.640	0.551	-0.682	-1.052	0.090	0.621
Male vs. Female		10.698**	2.848**	6.311*	5.303**	2.773**	5.796**

Sept.-1983-June 1984		Sept.	Oct.	Feb.	Mar.	May	June
Female	2 vs. 8	-0.639	-0.437	3.319*	1.762	0.088	-1.458
	7 vs. G	1.162	⌿ NS	⌿ NS	0.854	0.877	1.045
	1 vs. 7,G	1.477	1.121	2.277*	0.600	0.027	0.271
	2,8 vs. 1,7,G (Fed vs. Non-fed)	-0.566	2.003*	0.405	2.415*	2.481*	0.795
Male	2 vs. 8	0.725	0.283	-0.802	0.079	-1.438	0.818
	7 vs. G	0.819	⌿ NS	⌿ NS	0.985	0.346	0.346
	1 vs. 7,G	0.197	0.194	0.381	1.671	-0.031	0.214
	2,8 vs. 1,7,G (Fed vs. Non-fed)	0.144	0.709	1.207	2.094*	1.386	-0.990
Male vs. Female		4.017**	3.246**	6.916**	6.847**	-0.087	5.752**

x^2 tests between grids within treatments: Sept. 1981-Sept. 1983

Females: Fed grids, Grid 8 > rest for March 1982, x^2 = 15.53**; Non-fed grids = NS

Males: Fed grids = NS; Non-fed grids, Grid 1 > rest for April 1983, x^2 = 19.53**

Simplest Models which fit data: (Saturated = G,D,S,GD,GS,DS,GDS)

Date	Sex	Parameters omitted from model	L.R. Chi square	P-level
Sept. 1981-Sept. 1983	Combined	GDS, GS	8.29	0.217
	Female	None	0.00	1.000
	Male	GD	2.67	0.750
Sept. 1983-June 1984	Combined	GDS, GS	2.57	0.861
	Female	None	0.00	1.000
	Male	GD	13.12	0.593

⌿ No breeding evident on either grid, expected values = 0.

Table A4. Results of logit model tests (z values) on grid fidelity of adults and subadults; tests between treatments/grids and sexes by date. Significance levels: ** = 0.01; * = 0.05, (*) = 0.10.

September 1981-September 1983		1982				1983	
		Mar.	June	Aug.	Oct.	Apr.	Sept.
Male vs. Female	Pooled grids	-1.713(*)	0.596	1.070	1.230	-0.975	1.506
	Fed	-2.133*	-0.259	0.657	1.643(*)	0.041	1.829(*)
	Non-fed	-0.222	1.623(*)	0.987	-0.126	-1.493	0.154
Fed vs. Non-fed	Female	2.534*	3.256**	1.063	0.469	-1.011	-1.731(*)
	Male	0.703	1.805(*)	0.479	2.438*	0.576	-0.148

Oct. 1983-June 1984		Oct. 1983	Mar. 1984	Jun. 1984
Male vs. Female		0.806	-1.921*	-1.371
	Pooled over grids	1.160	-3.992**	-0.610
	Fed	-0.819	-2.936**	-1.027
	Non-fed	0.525	-1.737*	1.475
Female	Fed vs. Non-fed (2,8 vs. 1,7)	1.813(*)	2.373*	0.331
	G2 vs. G8	2.153*	1.659(*)	-0.335
	G1 vs. G7	0.446	2.955**	0.381
	2,8 vs. G	1.331	-1.076	-0.315
	1,7 vs. G	-0.164	1.751	0.128
Male:	Fed vs. Non-fed	0.223	1.884(*)	-2.139*
	G2 vs. G8	-0.219	-0.546	-0.461
	G1 vs. G7	0.730	2.006*	0.943
	2,8 vs. G	-0.258	-1.916(*)	-1.561
	1,7 vs. G	0.654	1.485	2.599**

x^2 tests between grids within treatments: Sept. 1981-Sept. 1983:

Non-fed grids: NS for either sex

Fed grids: lower male fidelity on grid 2, higher female fidelity on grid 8 in March 1982; lower male fidelity on grid 3 in Oct. 1982.

Simplest Models which fit data: (Saturated = G,D,S,GD,GS,DS,GDS)

Date	Sex	Parameters omitted from model	L.R. Chi square	P-level
Sept. 1981-Sept. 1983	Combined	GDS, GS	9.90	0.129
	Female	None	0.00	1.000
	Male	GD	3.73	0.590
Oct. 1983-June 1984	Combined	GDS, GS	12.86	0.379
	Female	None	0.00	1.000
	Male	GD	7.15	0.520

Table A5. Results of logit model tests (z values) on grid turnover rates of adults and subadults (% new captures); tests between treatments/grids and sexes by date. Significance levels: ** = 0.01; * = 0.05, (*) = 0.10.

September 1981-September 1983		1982				1983	
		Mar.	June	Aug.	Oct.	Apr.	Sept.
Male vs. Female	Fed	-0.158	1.155	1.852(*)	-2.035*	-2.249*	-1.130
	Non-fed	-0.849	-1.472	-0.839	0.884	1.750(*)	-0.127
Fed vs. Non-fed	Female	1.530	-1.968*	-2.666**	0.436	1.563	0.520
	Male	2.671**	0.518	-0.580	-2.617**	-2.484*	-0.699

Oct. 1983-June 1984		Oct. 1983	Mar. 1984	Jun. 1984
Male vs. Female	Pooled	1.404	0.854	-0.203
	Grassy	1.000	1.921(*)	1.371
	Fed	2.100*	0.400	0.447
	Non-fed	0.566	1.315	0.686
Female	Fed vs. Non-fed	4.535**	0.964	-0.930
	G2 vs. G8	0.027	1.229	-0.771
	G1 vs. G7	-1.998*	-0.093	-0.811
	2,8 vs. G	-0.249	-0.185	0.383
	1,7 vs. G	-3.531**	0.920	-1.017
Male:	Fed vs. Non-fed	5.542**	-0.937	-0.561
	G2 vs. G8	1.424	1.716	-0.729
	G1 vs. G7	-1.476	-2.732**	-0.564
	2,8 vs. G	2.437*	-2.105*	-1.377
	1,7 vs. G	-2.118*	-1.076	-0.994

x^2 tests between grids within treatments: Sept. 1981-Sept. 1983:

Non-fed grids: Significant difference in June, Aug. and Oct. 1982; grids and sexes inconsistent.

Fed grids: Significant difference in March, June, Oct. 1982; grids and sexes inconsistent.

Simplest Models which fit data: (Saturated = G,D,S,GD,GS,DS,GDS)

Date	Sex	Parameters omitted from model	L.R. Chi square	P-level
Sept. 1981-Sept. 1983	Combined	None	0.00	1.000
	Female	None	0.00	1.000
	Male	None	0.00	1.000
Oct. 1983-June 1984	Combined	GDS, GS	9.41	0.151
	Female	None	0.00	1.000
	Male	None	0.00	1.000

Table A6.   Results of logit model tests (z values) for injuries on separate grids in
1983–1984.   Significance levels: ** = 0.01, * = 0.05.

Comparison	1 9 8 3		1 9 8 4			
	Sept.	Oct.	Feb.	Mar.	May	June
Pooled over grids:						
Male vs. female	1.786	1.024	0.495	4.356**	−4.433**	−0.353
Grids (pooled over sexes)						
7 vs. G	−0.209	0.199	0.451	−0.130	0.461	0.386
1 vs. 7,G	−0.755	0.270	−1.302	4.537**	2.888**	1.152
2 vs. 8	0.518	0.633	−0.796	1.603	0.870	0.479
1 vs. 2,8	1.246	−0.564	2.140*	−0.250	−0.375	−0.156
2,8,1 vs. 7,G	0.078	−0.086	−0.651	5.099**	3.176**	1.397

Simplest Models which fit data: (Saturated = G,D,S,GD,GS,DS,GDS)

Date	Sex	Parameters omitted from model	L.R. Chi square	P-level
Sept. 1983– June 1984	Combined	G D S, G S	12.46	0.974
	Female	G D	15.05	0.860
	Male	G D	26.39	0.235

Table A7. Home range size estimates (75% and core area harmonic mean), sex, weights, and source of loss of radiotracked mice.

Mouse #/ Sex	Month	Wt. (g)	75% H.M.	Core Area	Mouse# / Sex	Month	Wt. (g)	75% H.M.	Core Area
Food-addition		WINTER					SUMMER		
3313 F	Nov.	19	198	119	2334 F	Jun.	24	2330	1040
3300 F	Nov.	20	569	370	3578 F	Jun.	26	2666	-
3245 F	Nov.	17	339	116	5324* F	Jun.	31	1681	929
5234† F	Nov.	22	105	24	3503* F	May	29	2604	-
5013 F	Feb.	17	220	127	5008* F	May	30	(26) eaten by weasel	
5017 M	Nov.	18	1481	975	4025+ M	Jun.	21	2020	1479
3468 M	Nov.	19	260	143	4036 M	Jun.	22	4663	-
5423+ M	Nov.	21	lost		5457+ M	May	23	lost	
5327 M	Feb.	18	452	-					
$\bar{X} \pm S$			453 ± 441					2661 ± 1048	
Control									
5056* F	Nov./Feb.	17	1317	786	3323 F	May	23	3534	-
5106 M	Nov.	17	2867	1769	3318 F	May	25	468	-
400* M	Feb.	19	3710	1464	4402 F	Aug.	17	3186	2415
200+ M	Feb.	18	514	294	4125 F	Aug.	19	2692	2022
300+ M	Feb.	18	1525	-	4406 F	Aug.	18	2730	1604
4001+ M	Feb.	17	lost		(4403) F	Aug.	20	lived on cliff 240 m from grid	
					2356 M	May	20	4338	-
					4202 M	Aug.	16	2273	1317
					4401 M	Aug.	18	(12558)	5916
					1001+ M	Aug.	20	lost	
$\bar{X} \pm S$			1987 ± 1282					3147 ± 1584	
Shrub-removal									
3528 F	Nov.	16	1600	776	1524 F	May	23	8615	6077
3535+ F	Nov./Feb.	17	3354	1217	5200 F	Jun.	24	1550	-
1515 F	Nov.	16	buried by snowplow		3556 F	Jun.	21	7503	-
2127 M	Nov.	18	1775	-	1428 M	May.	21	9333	5505
5167+ M	Nov./Feb.	20	1221	912	5157 M	May	23	5466	4192
1435+ M	Nov.	18	lost	-	2358 M	Jun.	24	6219	3874
					5201 M	May	22	10384	5990
$\bar{X} \pm S$			1988 ± 940					7010 ± 2956	

* confirmed predation

+ disappeared - unknown causes

† transmitted on Grid 7, moved to fed.

CURRICULUM VITAE

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Doctor of Philosophy

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